CONTRIBUTIONS IN MARINE SCIENCE

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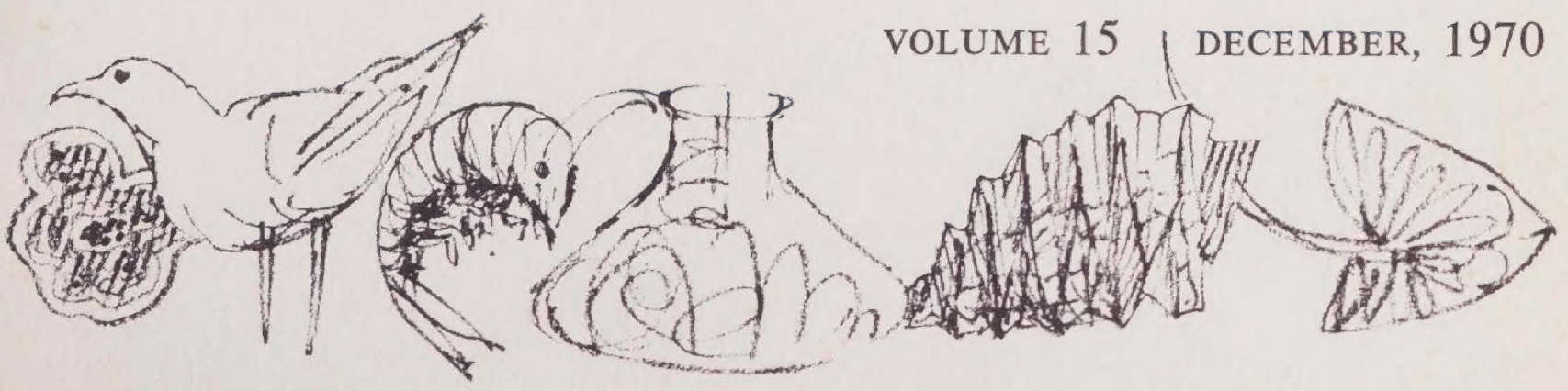

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 15, DECEMBER, 1970

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E. J. LUND, *age sixty-three.*

Elmer Julius Lund

1884–1969

Professor Lund's accomplishments and contributions to fellow scientists, former students and associates have been manifest in many positive ways. His contribution to the establishment of the Marine Science Institute is a high point of educational and research influence on the careers of many. These contributions were clearly revealed immediately upon my acquaintance with him as they had been to his friends and co-workers, who have continued to be greatly influenced by his pervasive magnetism.

Professor Lund was a brilliant, scintillating man who had a powerful intellectual influence on his students and professional colleagues. He had a superb skill in the conception and execution of experiments. His selection of the Port Aransas site for the Marine Science Institute at the juncture of the Gulf and the brackish to hypersaline array of bars and estuaries is but one example of his exceptional acumen in making far-reaching decisions. His masterful perceptiveness extended to matters in both scientific and civic affairs as the following tribute notes.

Donald E. Wohlschlag
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Elmer Julius Lund

E. J. Lund was born of Swedish parents on a Minnesota farm on 12 December 1884 and was named Hjalmar, which he later anglicized.

He grew up on the farm and went to high school nearby. At the age of fifteen he took over the management of the family affairs because of his father's illness. He worked at various jobs, including construction and threshing crews, to pay his way through school. In high school he took part in athletics on the track field, standing out especially in the high jump.

Due to the press of family business Lund did not enroll in college at an early age. He went to Hamline where he received the stimuli that set his course for life. He once told the first author that the first time he saw paramecium under the microscope and got a glimpse of the streaming protoplasm, he sat entranced all day and attended to nothing else. As a junior he became interested in animal light. As a result of his work he was invited in his senior year to join a Johns Hopkins group at Montego Bay, Jamaica. After finishing the Ph.B. degree at Hamline in 1910 he became a Bruce Fellow at Johns Hopkins in 1911, the same year that he published his first paper on fireflies and light. He remained a Bruce Fellow until 1914 when he received the Ph.D.

Johns Hopkins has been called the first real university in the Western Hemisphere, and at least it was the prototype of the German type university in America. In 1911 the department of biology still was under the heavy influence of W. K. Brooks who had died in 1910.

The people who influenced Lund most at Hopkins were H. S. Jennings, the botanist Burton Livingston, and S. O. Mast, but he worked essentially on his own. He said that at Hopkins in his day no one was interested in whether you were around or not except the bursar and the registrar. When questioned about whom he got his degree under he would say hesitantly that he took his thesis with Jennings. This was not from prejudice, but the fact that he worked on his own and Jennings' signature was simply a part of the ceremony. He once said that he took his degree with Freundlich's "Kapillarchemie."

After obtaining his degree Doctor Lund became an instructor in the University of Pennsylvania for one year in 1914. From 1915 to 1926 he was assistant and associate professor of zoology in the University of Minnesota where he established and taught the first course in general physiology in the United States. He was appointed professor of zoology in The University of Texas in 1926. While there he finally established a division of physiology and the department was called the department of zoology and physiology. After a long period of strife over this question the unit was renamed the department of zoology and Lund left the university in 1950.

Lund's interest in marine life began with his visit to Jamaica in 1911 and lasted throughout his life. From 1912 to 1916 he was instructor in zoology at the Woods Hole Marine Biological Laboratory and from 1918 to 1929 he was professor of physiology at the Puget Sound Biological Laboratory of the University of Washington during the summer. While on sabbatical from the University of Minne-

sota, in 1921–22 he worked in marine laboratories in France and England and Italy. While at the Stazione Zoologica di Napoli he tried to interest the German and other European professors in an abstract journal of the world biological literature, but had little success. Later he and other American professors founded Biological Abstracts and he was one of the section editors for many years.

When the Puget Sound Biological Laboratory was abolished after a factional fight within the parent university, Lund and the other famous professors who had taught there refused to return and Lund's interest was directed to the Gulf Coast.

Following a vast fish kill on the Texas coast in 1935, which we know now was caused by a Red Tide, Doctor Lund and the late Dr. A. H. Wiebe constructed a small rough lumber one-room shack on the Corps of Engineers dock at Port Aransas. This was the first marine laboratory erected in Texas and essentially the Institute of Marine Science (now Marine Science Institute) grew from it through Lund's nurture and on the same spot. He established a division of oceanography within the university and kept the marine laboratory idea alive throughout the war years. After the war he spent a great deal of time and energy hauling supplies, equipment and materials and supervising the construction of the early institute. He established Publications of the Institute of Marine Science and edited the first issue, which appeared in 1945. The second issue came out in 1950 after Professor Lund had left the University.

In spite of the fact that the founding of the Institute of Marine Science under very difficult conditions was a great contribution to the state and to the university, it was really only a side issue in Lund's professional life.

E. J. Lund was a good zoologist and he knew a great deal about the field. Nevertheless, he was an experimentalist first and last and he considered himself to be a physiologist. To this field he gave great loyalty and dedication. Essentially his interests were concerned with the cellular consumption of oxygen and the related energetics of this process. After his first few papers on light and on the consumption of food and the morphogenetic process in *Bursaria*, there followed a series of papers on intracellular respiration and oxidation. This led him to strong opposition of Child's theory of axial gradients, or "cephalization" as it is sometimes improperly called. The axial gradient ideas have died a natural death and faded away.

Lund's conceptualization of apparatus and techniques with which to carry on experiments was always a source of wonderment to students. His inventiveness and his questioning mind led him to work on bioelectric currents and his first paper was published in 1921. He found that weak, non-lethal electric currents could stimulate or retard the growth of *Obelia*. Later he showed that these currents could influence the direction of growth and still later on he showed that the currents had a specific polarization in connection with the anatomy and cellular structure of the organism.

Lund and his students carried these ideas much further in connection with the growth of onion roots and oat coleoptiles as related to gravity, the influence of light and the distribution of glutathione, oxygen consumption, oxidation-reduction systems and other polarities of the living systems.

He advanced the thesis, well-documented with experimental data, that all living, growing systems possess an inherent bioelectric field operating as a mechanism of correlation in the absence of hormones or nervous systems. To account for the origin of the bioelectric field, as well as the mechanism of production of continuously maintained bioelectric potential differences and currents, he developed the oxidation-reduction theory of origin of electric polarity of cells. The electromotive materials were conceived to be intermediates in the normal respiratory metabolism maintained at flux equilibrium by constant rates of production and conversion, and manifesting their electric potentials at cellular phase boundaries. While the oxidation-reduction theory of origin of bioelectric potential differences has had a mixed reception, its clear emphasis upon the immediacy of the relations between respiratory metabolism, potential differences, growth control, cell polarity of structure and function, has had an impressive impact, often unacknowledged, not only on the development of these areas of physiology and biophysics, but also upon others, such as ion distribution and movement, active transport, and energy coupling.

These remarks are a brief summary of Lund's great contribution to physiology, which was partially summarized in his book, "Bioelectric Fields and Growth", 331 pp., University of Texas, Press, 1947.

In the late 50's Doctor Lund became interested in the physiology of the oyster and published five papers on that subject. His most omportant ideas concerned self-silting and the significance of the oyster and other filter feeding organisms to sedimentation.

In the older editions of the American Men of Science, Doctor Lund was "starred" as being among the first 1,000 scientists in North America. He was elected the sixth Honorary Professor at The University of Texas in 1932.
He was invited to give the research lectures in plant physiology at Purdue University and was awarded the honorary Doctor of Science degree by Hamline University in 1935. He was invited to two International Congresses on Cytology to lecture on bioelectric phenomena in London and Cambridge.

He was a most inspiring teacher who used to hold his students spellbound long after the class hour was over. He turned out sixteen doctoral students who hold responsible positions all over the United States. The intense concentration of the man and his scintillating dedication to the field of general physiology are impossible to describe, but the memory of these things will remain with his students to the end of their lives.

He was married to the late Barbara Lee for 42 years and later to Dr. Hilda Rosene who survives him. He had no children. He died at his home in Port Aransas, Texas on 28 November 1969.

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DISTRIBUTION OF JUVENILE BROWN SHRIMP (*PENAEUS AZTECUS* IVES) IN GALVESTON BAY, TEXAS, AS RELATED TO CERTAIN HYDROGRAPHIC FEATURES AND SALINITY

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ABSTRACT

A survey of juvenile brown shrimp, *Penaeus aztecus* Ives, was conducted in Galveston Bay during 1963 and 1964 to determine where they were concentrated, to establish their movement patterns, and to determine to what extent salinity effects their distribution.

Upon entering the bay, these shrimp were found concentrated primarily along the shores and in the marshes and bayous. Re-distribution did not occur until Gulfward emigration began. The path of emigration appeared to be along a direct route to the passes and not the result of a random search. Size at emigration varied between 70–100 mm. Shrimp were abundant at salinities from 0.9 ot 30.8 ‰ and it was concluded that salinity *per se* had no detectable effect on distribution.

INTRODUCTION

Because of the increasing importance of the brown shrimp (*Penaeus aztecus* Ives) to the commercial fishery of the Gulf coast, considerable effort has been devoted to the study of its ecology, both in the inshore Gulf and the adjoining bays. This species spawns in the Gulf and in the early spring the postlarvae move into the shallow estuaries and lagoons where they grow to the juvenile stage before returning to the sea. Although the principle commercial fishery exists in the Gulf where the adults reside, a sizeable bait shrimp fishery is supported within the bays (Chin 1960). Rapidly expanding industrial and municipal water needs have resulted in an increasing demand for the waters of these shallow bays. With proper management, these needs can be met without reducing the carrying capacity of the bays for shrimp.

To facilitate future management of estuarine water for this species, a survey of juvenile brown shrimp was conducted in Galveston Bay during 1963 and 1964. The purpose of this survey was to (1) determine where these shrimp were concentrated, (2) establish their movement patterns and (3) determine to what extent salinity affected their distribution.

DESCRIPTION OF THE AREA

The study area (Fig. 1), located on the upper Texas coast, included about 385

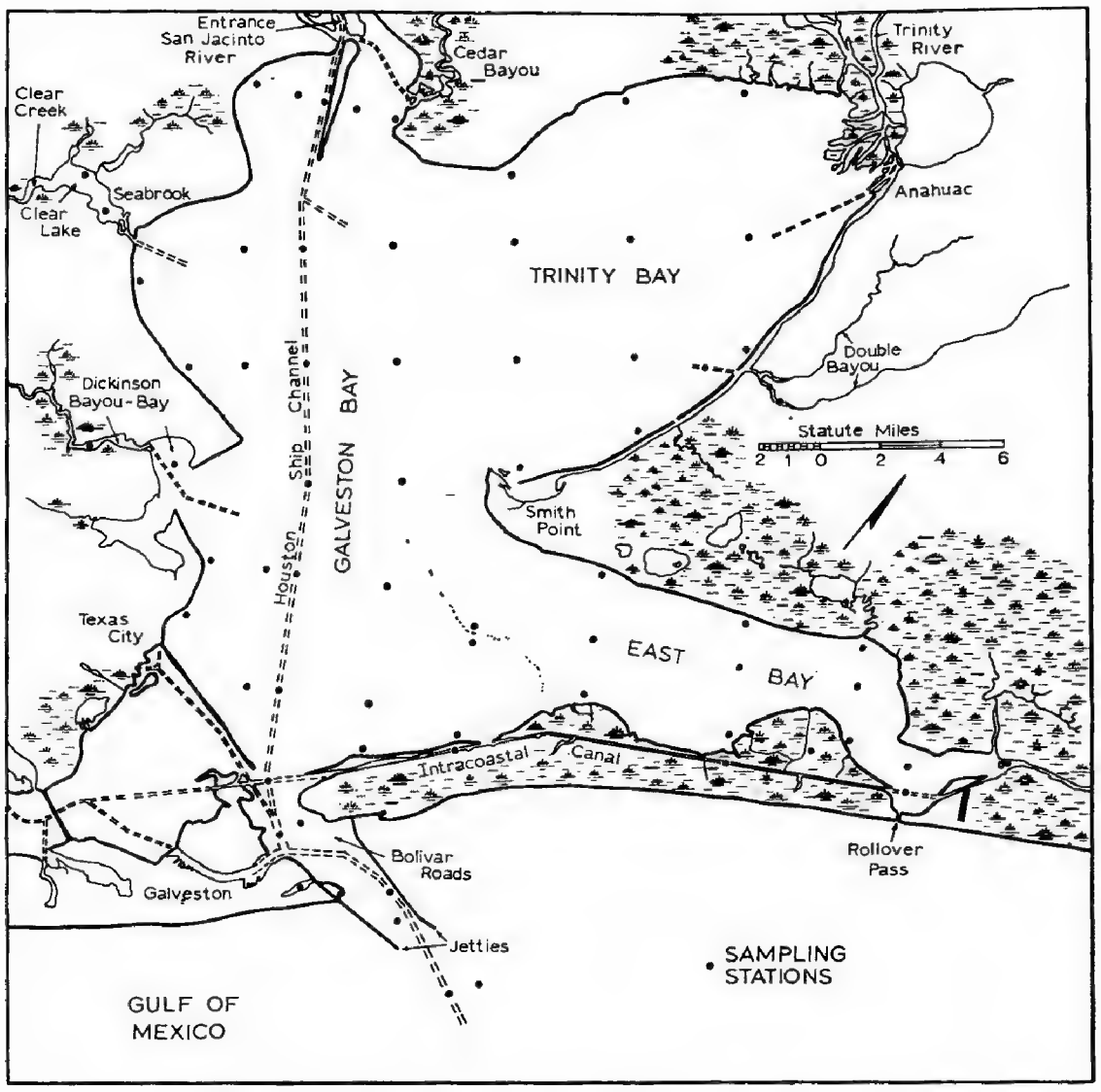

FIG. 1. Map of study area with the location of sampling stations.

square miles of the Galveston Bay System in addition to a small portion of the Gulf of Mexico just outside the Galveston jetties. A large jettied and dredged natural pass (Bolivar Roads) and a small man-made channel (Rollover Pass) provide access to the Gulf. Most of the fresh water is supplied by the Trinity and San Jacinto Rivers. Of the four major bays within this estuary—Trinity, Galveston, East and West Bays—only the first three were included in the study area, and a description of each is given below.

Galveston Bay

This is the largest bay within the system. Its waters cover about 193 square miles and range in depth up to 16 feet (excluding dredged channels). The Houston Ship Channel (42 feet in depth) extends the length of this bay and provides passage to the city of Houston for ocean-going vessels. Because of its size, this bay has been subdivided into upper and lower portions and will be considered accordingly hereafter.

Upper Galveston Bay which is in the upper northwest quadrant covers approximately 100 square miles. The San Jacinto River enters at the head of this bay, as do two major streams—Clear Creek and Cedar Bayou. A marsh complex extends along much of the shoreline in the Clear Creek-Clear Lake area and also along the

Cedar Bayou shore. The shoreline is heavily populated and highly industrialized.

Lower Galveston Bay covers about 93 square miles and is in the southwest quadrant. Bolivar Roads, which serves as a passageway for Galveston and Houston ocean-going shipping, connects it with the Gulf. Dickinson Bayou provides the only direct source of freshwater. A marsh complex extends along the shoreline of Dickinson Bayou and Dickinson Bay. The shoreline of this bay is heavily populated and highly industrialized.

Trinity Bay

The waters of this bay, ranging in depth up to 10 feet, cover about 139 square miles and extend from the headwaters of the Trinity River southwest to Smith Point. A marsh complex extends along the eastern shoreline and encompasses much of the Trinity River delta. The shores are sparsely populated, but an immense oil field has been developed in the bay and new wells are continually being drilled. Aside from the Trinity River, a number of small bayous supply additional fresh water to this bay.

East Bay

East Bay has an area of about 51 square miles and a maximum depth of seven feet. It is in the southeast quadrant and is a typical Texas coastal lagoon. An extensive marsh complex extends along almost the entire shoreline and from this marsh a number of small brackish-water bayous flow into the bay. Additional brackish water is supplied to East Bay through the Gulf Intracoastal Waterway which drains much of the marsh area to the northeast. Rollover Pass connects East Bay with the Gulf, but according to Reid (1957), water flow is restricted and probably affects only the very eastern end of the bay. The shores of this bay are sparsely populated, and it, of the three, is least disturbed by man-made development projects.

METHODS

Beginning in January, 1963, brown shrimp were collected at 65 stations (see Fig. 1) twice monthly with a small shrimp trawl. Stations were established in the marginal areas of the system (lakes, bayous, marshes and the Intracoastal Canal), the shores (waters of the bay proper where depth was less than 4 feet), the open bay, the Houston Ship Channel, the Bolivar Roads tidal pass and the Gulf just outside the pass. At each station, bottom salinity was measured and an otter trawl, measuring 10 feet between the boards with 1⅜-inch stretched mesh in the body and 1-in stretched mesh in the cod end, was fished for 5 minutes. Sampling was usually initiated on or about the 5th and 20th of each month. Three days were generally required to visit all stations. The frequency of sampling was reduced to once monthly in March 1964, and samples were taken around the 15th of each month.

Trawl samples were placed in plastic bags containing 10% ethyl alcohol preservative, stored in ice and brought to the laboratory where the brown shrimp were removed and counted. Each specimen was measured to the nearest 0.1 gram on a Mettler balance (Type K-7, precision ± 0.05 g). The total weight of the shrimp in each sample was also measured. Where a large number of individuals were present in a sample, a subsample was taken from which the individuals were counted and weighed. The ratio of subsample weight to sample weight equated the subsample to the sample. On randomly selected shrimp, both total length (tip of the rostrum to

tip of the telson) and weight were measured. These observations were used to determine length-weight relationships from which weight was converted to length (Parker 1965).

Salinity was measured with an RS-5 portable salinometer made by Industrial Instruments, Inc. This is a direct reading, battery-operated instrument designed to measure salinity, electrical conductivity, and temperature at water depths up to 300 feet with an accuracy of ±0.3‰, ±0.05 millihos/cm, and ±0.5°C, respectively. A measure of electrical conductivity and temperature is necessary to determine salinity. A modification of Knudsen's method of salinity determination (Marvin, Zein-Eldin, May and Lansford 1960) was used periodically to check the accuracy of the meter. When a meter malfunctioned, water samples were obtained with a Kemmerer water sampler, and salinity was determined by Knudsen's method (modified).

SEASONAL ABUNDANCE

According to Berry and Baxter (1967), mass migration of brown shrimp postlarvae into Galveston Bay in 1963 began in early March. My catches first contained brown shrimp (juveniles) in early April (Fig. 2). These juveniles were most abundant in late May. Catches declined notably during the next 4 weeks as shrimp began emigrating to the Gulf. Thereafter, catches declined gradually until late December when no shrimp were captured.

Berry and Baxter (1967) did not observe mass movement of postlarvae into the system again until mid-March, 1964 (about 2 weeks later than in 1963), and my catches did not contain juveniles until mid-May. Catches were again highest in May and declined thereafter as in 1963. The period from March, when postlarvae enter, through June, when most of the juveniles emigrate, constitutes the brown shrimp season in Galveston Bay.

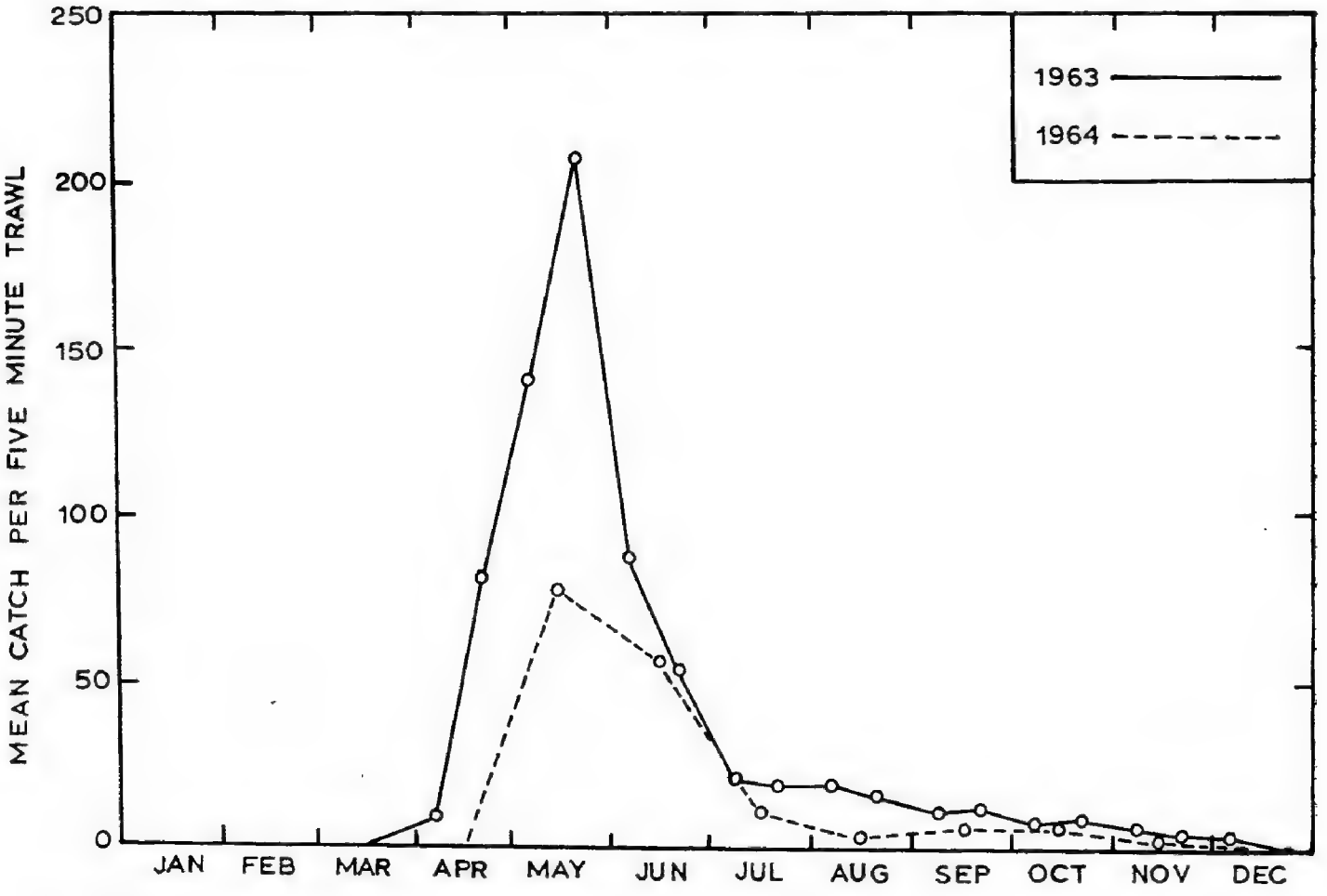

FIG. 2. Relative abundance of juvenile brown shrimp in Galveston Bay, Texas, during 1963 and 1964, as indicated by mean trawl catch.

A comparison of catch between years revealed significantly greater numbers during 1963 in April (no statistical tests were performed since April catch in 1964 was zero) and May ($t = 3.887$, d.f. $= 63$ for early May 1963 against May 1964; $t = 4.985$, d.f. $= 63$ for late May 1963 against May 1964)[1]. If the area between the relative abundance lines in Figure 2 is considered, the difference in catch between years during April and May indicates a sizable reduction in the population in 1964. Baxter (1965) noted a similar reduction in brown shrimp from the Galveston Bay bait fishery from 1963 to 1964, and attributed it to a reduction in the number of postlarvae he observed entering at the passes during 1964.

DISTRIBUTION AND EMIGRATION

The distribution of juveniles within the system throughout the period of peak abundance in 1963 and 1964 is shown by time in Figure 3. The data from August through December were omitted because they were similar to or less informative than that of July.

In 1963, juveniles first appeared in early April along the southeastern shore of Trinity Bay and throughout East Bay. By late April, they were present in all areas except along the Houston Ship Channel and this area was populated by early May. From late April through late May, concentrations were highest along the shores and marshes of East and Trinity Bays. High numbers were also observed in Upper Galveston Bay, Dickinson Bay and Bayou, and Clear Lake. These areas appear to constitute the principle nursery areas for brown shrimp in this estuarine system. Emigration to the Gulf began in late May and, as evidenced by the drastic reduction in numbers, reached its peak in early June. Except for a few stragglers, emigration was completed by early July.

Although somewhat less detailed in 1964, when sampling was conducted only once monthly, dispersion apparently followed the same pattern as in 1963.

The configuration of these relative abundance patterns and the short time over which mass emigration occurs suggest that during the period of peak emigration the path is along a direct route to the passes and not the result of a random search. Inglis (1960) presented information on marked brown shrimp released in Clear Lake which also suggests a direct gulfward emigration route. Of 71 recaptures taken farther than two miles from the Clear Lake Channel, 75 percent (54) were taken along the most direct gulfward route (including three captured in the Gulf).

Size is apparently an important factor regulating emigration. Ringo (1965) found that postlarvae (10–25 mm), upon entering the system, concentrated in the shallow waters. In 1963, my catches revealed that the smallest shrimp (25–40 mm) also concentrated primarily in these shallow peripheral zones (Fig. 4). These concentrations continued to build as size increased and extended well into the open bay for 41–45 mm and 56–70 mm shrimp. The configuration of the distribution pattern, however, remained unchanged, indicating no appreciable re-distribution. Evidence of mass movement, probably to the Gulf, first appeared in the 71–85 mm group, whose numbers decreased considerably in East, Dickin-

[1] A paired t-test was used and pairing was by station location.

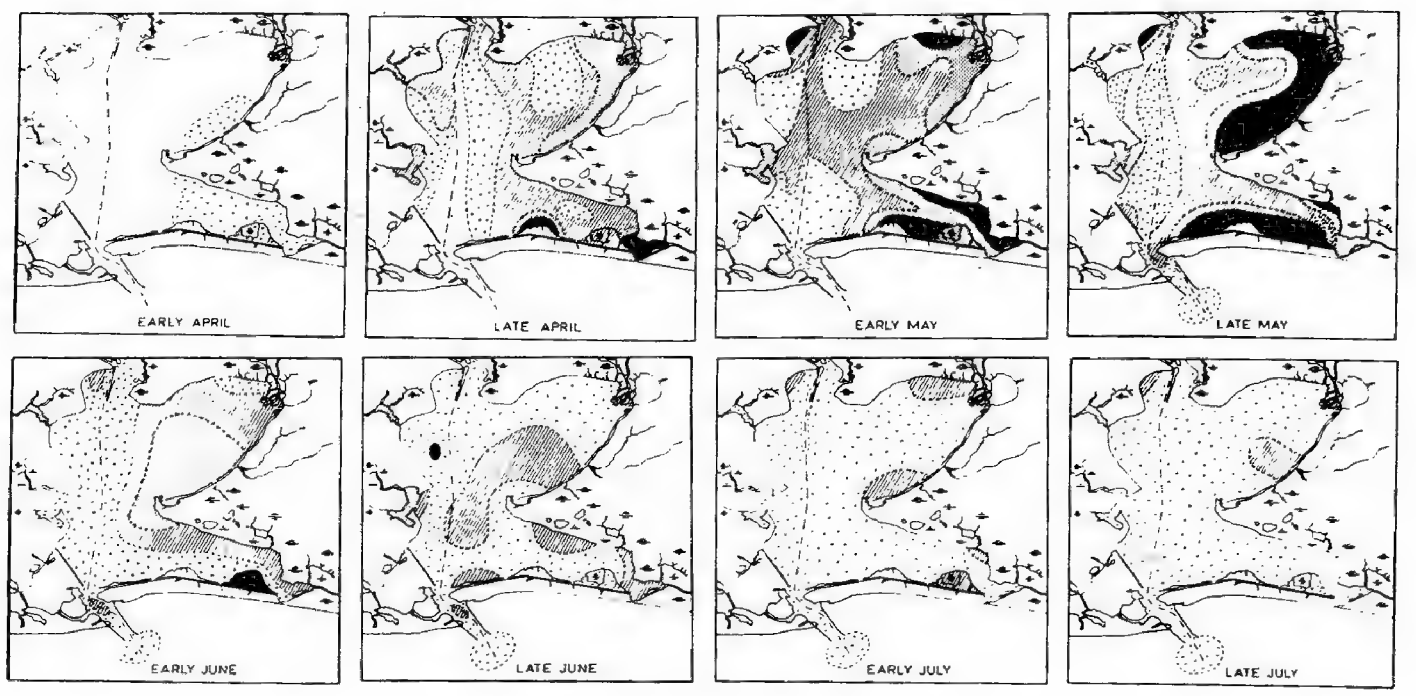

FIG. 3. Distribution of juvenile brown shrimp in Galveston Bay, Texas, during the periods of peak abundance in 1963 and 1964 as indicated by relative abundance.

son and Upper Galveston Bays and shifted gulfward in Trinity Bay. Mass emigration through Bolivar Roads was evident for 86–100 mm shrimp. The exodus from the peripheral and shore zones and from the bay itself continued with increasing size. Shrimp larger than 130 mm were found only in the deeper waters and near the passes. In 1964, the distribution pattern was similar, but no appreciable evidence of a gulfward movement was apparent until shrimp reached the 86–100 mm size group. In fact, this was the first size group to appear in the Gulf, whereas in 1963, 41–55 mm shrimp were found in the Gulf.

Trent (1966) observed that the mean length of brown shrimp emigrating through the Bolivar Roads tidal pass from May-August, 1966, increased with time according to the relationship $L = 3.16\ T + 65.89$ (whree L = total length in mm and T = time in weeks), and he observed peaks of emigrating shrimp during May and June. No evidence is available concerning population density in the bay during the period of his study, but it is possible, in view of differences in

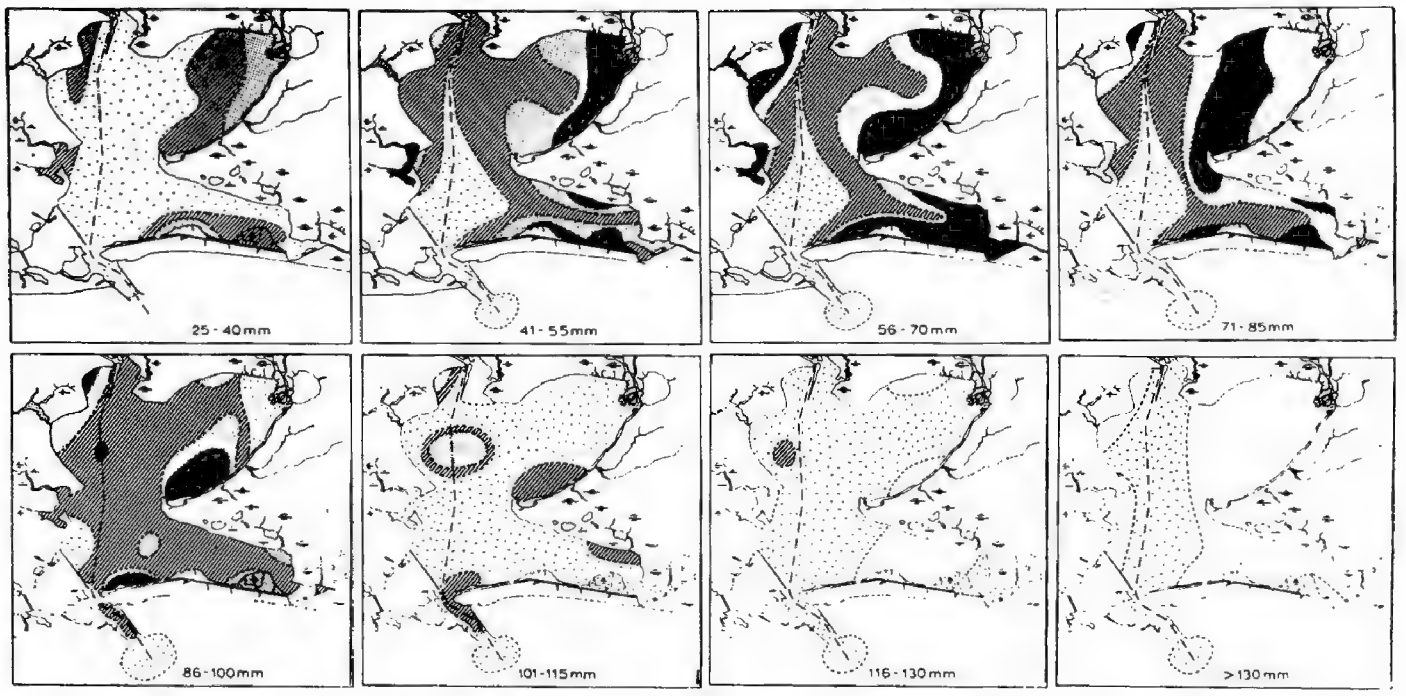

FIG. 4. Distribution of size classes of juvenile brown shrimp in the Galveston Bay System, Texas, in 1963 and 1964 as indicated by relative abundance.

relative abundance in 1963 and 1964 that density within the bay was a factor regulating time of emigration and size at emigration. Certainly if the bay were populated well below its maximum capacity, as appeared likely in 1964, juveniles could remain in the nursery areas longer because of more available food and, consequently, grow to a larger size before emigrating to the Gulf.

TABLE 1

Relative abundance of brown shrimp in Galveston Bay in 1963 and 1964 as related to salinity.

	Salinity %	Number of Hauls	Number Caught	Mean Catch Per Tow
1963	0– 4.9	15	1,672	111.5
	0– 9.9	47	3,110	66.2
	10–14.9	108	5,010	46.4
	15–19.9	255	11,301	44.3
	20–24.9	349	12,533	35.9
	25–29.9	132	1,791	13.6
	> 30	27	407	15.1
	Total	933	35,824	38.4
1964	0– 4.9	21	509	24.2
	5– 9.9	18	671	37.3
	10–14.9	75	2,460	32.8
	15–19.9	136	3,554	26.1
	20–24.9	126	1,843	14.6
	25–29.9	50	792	15.8
	> 30	5	2	0.4
	Total	431	9,831	22.8
Two Years Combined	0– 4.9	36	2,181	60.6
	5– 9.9	65	3,781	58.2
	10–14.9	183	7,470	40.8
	15–19.9	391	14,855	38.0
	20–24.9	475	14,376	30.3
	25–29.9	182	2,583	14.2
	> 30	32	409	12.8
	Total	1,364	45,655	33.5

DISTRIBUTION AS RELATED TO SALINITY

Zein-Eldin (1963) has pointed out that neither the stimulus for gulfward migration of young brown shrimp nor the factors controlling the period of time they spend in the estuaries and lagoons are well understood. Salinity *per se* has been considered by many to be of prime importance, yet no evidence is presently available to indicate that immature brown shrimp cannot thrive and grow in salinities ranging between 1 and 35‰. The relation between salinity and the distribution of penaeid shrimp in Gulf of Mexico waters has been discussed by Gunter, Christmas and Killebrew (1964), where special reference was made to the brown shrimp, *Penaeus aztecus*, in Texas coastal waters. They found young brown shrimp in greatest abundance within the salinity range of 10 to 30‰, and they observed considerably higher numbers in salinities above 20‰ than in salinities below 10‰. Their findings were based on trawl catches combined from all estuarine systems along the Texas coast. These systems exhibit varying saline conditions ranging from the consistently low salinities of Sabine Lake to consistently high salinities of the Laguna Madre. Since shrimp populations within

these estuaries are geographically isolated and react independently, it should be more informative to study this relationship in a single system exhibiting a wide salinity range. For this reason, the relation between salinity and the distribution of brown shrimp was examined in considerable detail in Galveston Bay.

The isohalines during the period when shrimp were abundant in 1963 and 1964 are presented in Figure 5. Juvenile brown shrimp in this system encountered waters where bottom salinity ranged between 0.9 and 36.5‰. Incidentally, 0.9‰ was the lowest salinity at which brown shrimp have been reported in Texas coastal waters and 658 individuals were collected in one five-min tow. The bulk of the population is present in the system from March through June, the time of year when the salinities are generally low. Presenting my data in a manner comparable with those of Gunter, Christmas, Killebrew (1964), I observed (Table 1) the greatest mean catch per five-min tow during 1963 in salinities less than 5‰. Above 5‰, catch declined with increasing salinity. In 1964, mean catch per tow was highest in salinities between 5 and 10‰ and above 10‰, catch again declined with increasing salinity. In contrast to the findings of Gunter, Christmas and Killebrew (1964), catches averaged over the two-year period indicated that these shrimp were most abundant in salinities less than 5‰ and in salinities above 5‰ abundance declined with increasing salinity.

The inconsistency of these findings and the fact that sampling was not equivalent within salinity classes in either study leads me to conclude that results obtained from trawl data compiled in this manner are misleading when evaluating the effect of salinity on distribution. In Galveston Bay, the high catch per tow at salinities below 5‰ resulted because these salinities occurred only during the period of peak abundance and in an area where shrimp were abundant. Shrimp were just as abundant in other areas of higher salinity, but the catch there was averaged with catches from equally saline areas of low abundance.

By cross referencing Figures 3 and 5, it is evident that within each of the four major subdivisions of the system, the regions of high shrimp abundance also generally maintained the lowest subareal salinities. This does not, however, necessarily imply a salinity-oriented distribution. According to Table 2, which contains the salinity and catch of brown shrimp at stations where I considered them abundant, these shrimp were abundant in salinities throughout the range from 0.9 to 30.8‰. Coupling this information with the fact that shrimp hatch and develop to postlarvae in sea water (approximately 35‰ salt) and juveniles return to sea water upon leaving the bay, I concluded that, given adequate time to acclimate, young brown shrimp can thrive in abundance in salinities from 0.9 to 35‰.

Accordingly, the findings of this study indicate, as did Hoese (1960), that within certain areas, salinity in broad ranges is inconsequential to young brown shrimp. A further indication of the relative unimportance of salinity over the range encountered in this study was noted by Zein-Eldin (1963) who stated that: "Postlarval shrimp (penaeid—no species differentiation) can both survive and grow over a wide range of salinities. Thus, it would appear that salinity tolerances *per se* may not play a direct role in the growth and survival of postlarval and juvenile shrimp in the estuarine environment." In view of the high concentra-

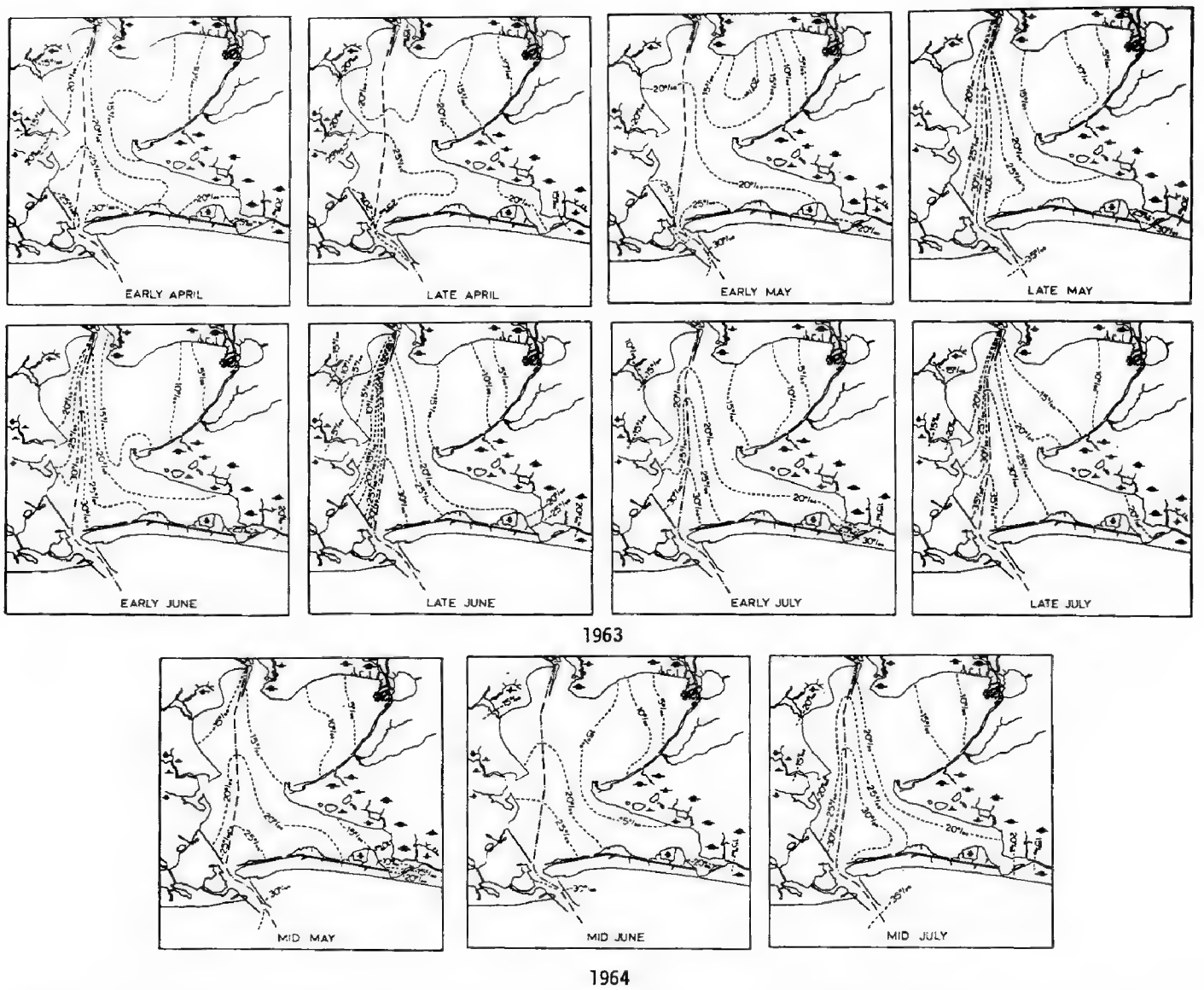

FIG. 5. Isohalines of the Galveston Bay System, Texas, in 1963 and 1964 during the period when brown shrimp were abundant.

TABLE 2

Salinity and catch per 5-minute tow of brown shrimp in Galveston Bay, Texas, during 1963 and 1964 at stations where they were assumed abundant (more than 250 shrimp caught per 5-minute trawl).

Salinity (%)	Catch	Salinity (%)	Catch
0.9	658	19.4	348
2.7	527	20.1	287
6.3	303	20.8	452
8.2	350	21.0	320
9.6	391	21.4	296
11.4	389	22.1	453
12.0	345	22.8	289
13.8	529	22.9	567
14.1	269	23.4	308
16.3	251	23.4	486
16.9	384	23.6	288
17.3	264	24.2	355
17.4	380	24.4	624
17.4	565	24.9	831
18.6	357	27.4	318
18.9	383	30.8	839

tions of young shrimp observed in the peripheral and shore zones of Galveston Bay, food requirements, as suggested by Zein-Eldin (1963) or protection from predators, as suggested by Hoese (1960) were likely of more importance than salinity *per se*.

SUMMARY

1. A comparison of 1963 and 1964 trawl catches indicated a sizable reduction in numbers in 1964.

2. The distribution of juvenile shrimp followed a rather distinct pattern during both years. The smallest shrimp concentrated in the peripheral and shore zones. The configuration of this pattern and the short time over which mass emigration occurs indicated that the path of emigration was along a direct route to the passes and not the result of a random search.

3. In 1963, mass emigration was first evident in 71–85 mm shrimp, whereas in 1964, no appreciable evidence of emigration was apparent until shrimp reached 86–100 mm. This difference in size at emigration could have been caused by the reduction in numbers during 1964 which resulted in more available food and consequently longer utilization of the nursery areas.

4. The distribution patterns of juveniles in the system indicates that portions of East, Trinity, and Upper and Lower Galveston Bays serve as principle nursery areas.

5. Juvenile brown shrimp were abundant throughout the salinity range 0.9 to 30.8‰, and it was concluded that salinity *per se* had no detectable effect on their distribution.

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The author wishes to express his appreciation to personnel of the Bureau of Commercial Fisheries, Galveston, Texas, who assisted him in collecting, processing, and tabulating the data used in this study. Of these, he is most especially indebted to Messrs. Cornelius R. Mock, Edward J. Pullen, Robert D. Ringo and Gilbert Zamora, and Mrs. Genevieve Adams.

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NORMAL ALKANES OF FIVE COASTAL SPERMATOPHYTES

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ABSTRACT

The alkanes of five marine grass-like plants which occur on the coast of Texas were characterized by infra-red spectroscopy and identified by gas-liquid chromatography. These fractions constitute approximately 0.01 % of the dry weight of *Thalassia testudinum* Konig and Sims (turtle grass), *Halophila engelmanni* Aschers, *Diplanthera wrightii* Aschers, and *Syringodium filiforme* Kutzing which is also *Cymodocea manatorum* Aschers (manatee grass). Alkanes were seven times more abundant in *Ruppia maritima* L. (widgeon grass) than in the other four plants. The plants contained various mixtures of normal hydrocarbons with 15 to 31 carbon atoms. The chromatographic techniques could not detect normal hydrocarbons with more than 36 carbon atoms or less than 11. The distributional patterns of the normal alkanes suggest the relative distinctiveness of each taxonomic group.

INTRODUCTION

Five marine vascular plants form vast grassy meadows over soft sand bottoms of shallow water bays and lagoons and in other shoal-water envirnoments along the coasts of the Gulf of Mexico (Thorne 1954). These plants are able to withstand salinities of at least 60‰ (McMillan and Moseley 1967): *Ruppia* occurs in brackish water as well as in fresh water ponds throughout the western United States (Muenscher 1944). Phillips (1960) supports the suggestion that "sea grasses" are important in building highly organic lagoonal deposits by trapping sediment and detritus which is difficult to resuspend once it has settled into the root mat of the plants. Since reducing conditions prevail near the sediment surface in many such shallow lagoons and since sediments tend to be preserved under protection from the open Gulf by barrier islands, similar environments may build up in geologic time significant organic deposits. As substantial contributors of organic debris, these "grasses" produce high molecular weight hydrocarbons which are often considered to be characteristic of terrestrial plants (Clark and Blumer 1967).

The fatty acids of these plants were studied by Maurer and Parker (1967) who found unbranched saturated fatty acids containing 14, 15 and 16 carbon atoms. Unsaturated acids containing 16 and 18 carbon atoms were also abundant. The

presence of normal alkanes with chains of 15 to 31 carbon atoms does not reflect a simple decarboxylation of their fatty acids as a biosynthetic pathway.

The presence in the representatives of Zannichelliaceae and Ruppiacea of hydrocarbons of greater molecular weight than in Hydrocharitaceae has systematic significance.

EXPERIMENTAL

The plants with the exception of *Ruppia* were collected by hand in one to five feet of water in Redfish Bay, Texas, during October. *Ruppia* which was collected in a brackish pond south of Port Aransas during the same month was in flower. The plants were dried in air or a vented oven at 45°. The dry material was extracted with redistilled hexane in Soxhlet extractors. Lipids were saponified in 0.5 N methanolic KOH. Nonsaponifiables were removed from saponification mixtures by extraction into ethyl ether.

Hydrocarbons were separated in iso-octane from the remainder of the nonsaponifiables as the first fraction from a column of silica gel (Woelm).

Gas-liquid chromatography was done on a Perkin-Elmer 880 gas chromatograph equipped with hydrogen-flame detectors. Dual columns (¼ in x 6 ft) packed with 5% FFAP on Chromosorb G (60/80 mesh) were used. The temperature was programmed from 114° to 270° at 4° per minute. Helium flowing at 35 ml/min under 50 psi was the carrier gas. The chromatography was repeated on the same instrument using the same flow rate and columns of the same size packed with 5% Apiezon L on Chromosorb G (60/80 mesh). The temperature was programmed from 125° to 290° at 4° per minute. Each hydrocarbon fraction was coinjected with a standard hydrocarbon mixture containing nine normal alkanes. The abundance of each component was determined by its corresponding peak area in the gas chromatograms. Peak areas were established by multiplying peak height by peak width at half height.

Infra-red spectra were measured on a Perkin-Elmer 237B Spectrophotometer.

RESULTS AND DISCUSSION

The infra-red spectra of the hydrocarbon fractions showed absorption bands for carbon-hydrogen stretching vibrations at 2850 cm^{-1}, 2900 cm^{-1}, and 2950 cm^{-1} and bands for the carbon-hydrogen deformational vibrations of the $C\text{-}CH_3$ grouping at 1380 cm^{-1} along with those of the $\text{-}CH_2\text{-}$ group at 1465 cm^{-1}. The characteristic double band from skeletal vibrations of long saturated hydrocarbon chains appeared at 725 cm^{-1}. There are no bands indicating the presence of carbon-carbon double bonds or functional groups containing oxygen atoms. Figure 1 shows the infra-red spectrum of alkanes from *Diplanthera wrightii*. Hydrocarbon fractions from the other plants exhibited similar infra-red spectra.

Table 1 shows the relative amounts of lipids, nonsaponifiables, and hydrocarbons in the plants. *Ruppia* is by far the richest in hydrocarbons.

Qualitative comparisons of the hydrocarbons fractions can be made by looking at Figures 2, 3, 4, 5 and 6 which show chromatograms for the fractions.

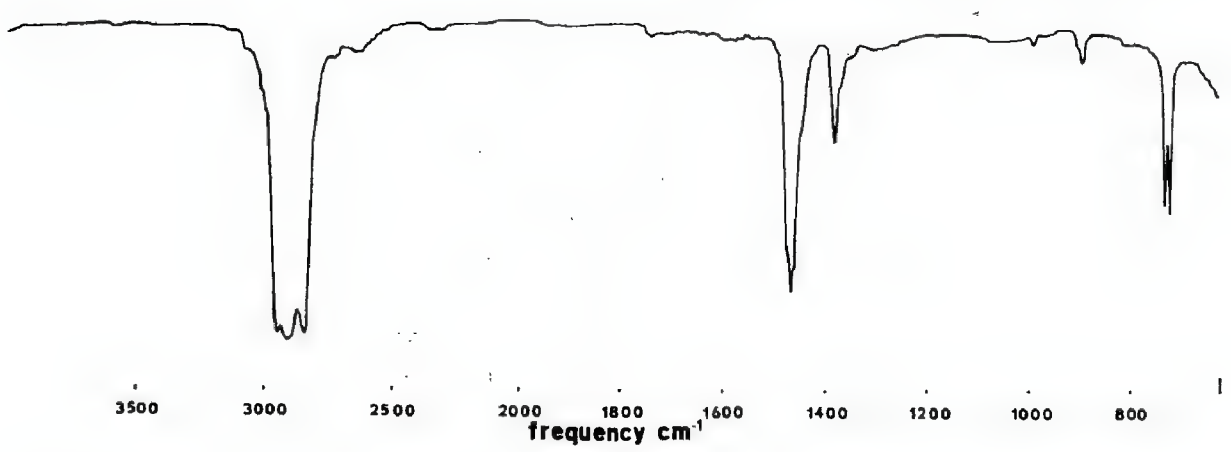

FIG. 1. Infra-red spectrum of alkane fraction isolated from *Diplanthera*. (Neat)

TABLE 1

Percentage of Lipids, Nonsaponifiable Material and Hydrocarbons in Five Marine Spermatophtyes (based on dry weight)

Genus	Lipids	Nonsaponifiables	Hydrocarbons
Syringodium	1.1	0.3 (estimated)	0.011
Diplanthera	1.2	0.20	0.010
Ruppia	2.2	1.0	0.073
Halophila	1.5	0.22	0.008
Thalassia	1.1	0.41	0.010

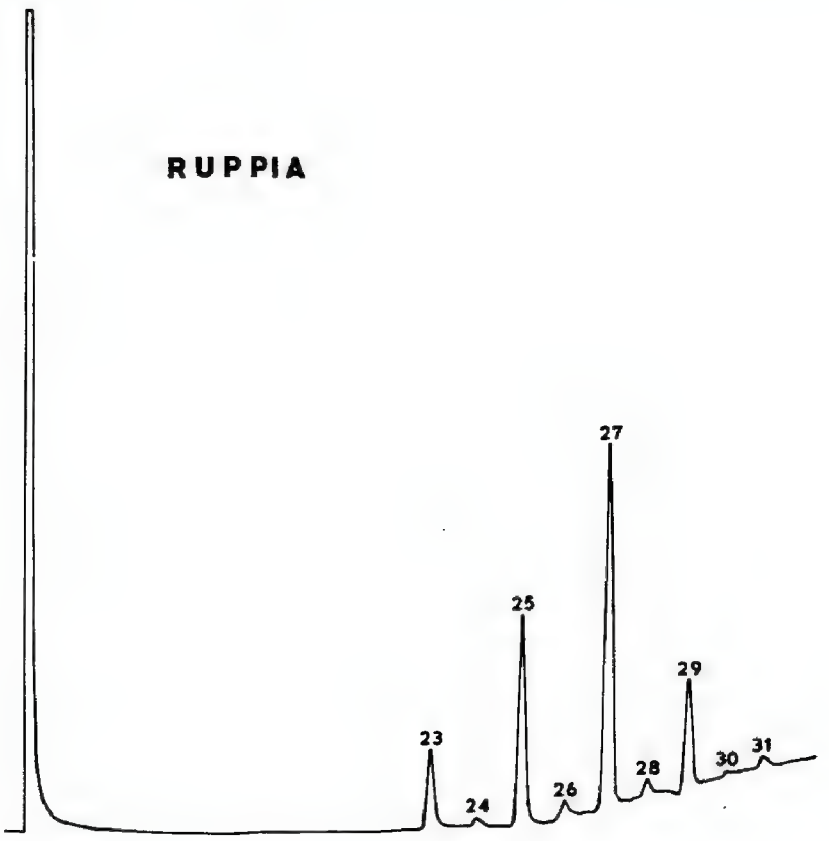

FIG. 2. Gas chromatogram of alkane fraction isolated from *Ruppia*. Numbers indicate the number of carbon atoms in the compounds corresponding to the peaks. Operating conditions: 5% FFAP on Chromosorb G (60/80 mesh); temperature was programmed from 125° to 290° at 4° per minute; helium was flowed at 35 ml/min.

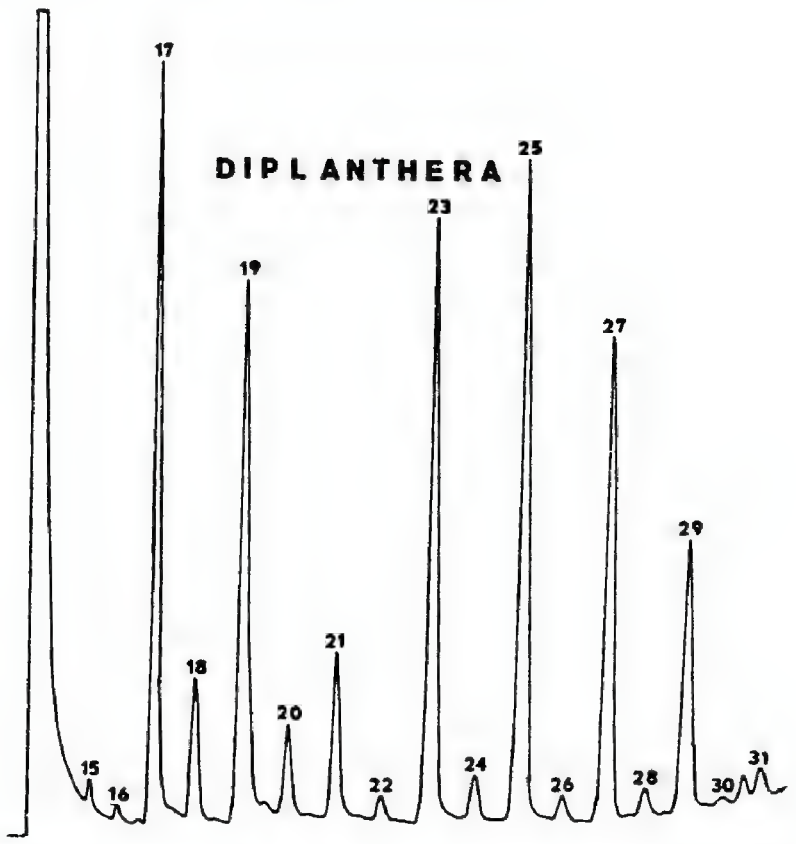

FIG. 3. Gas chromatogram of alkane fraction isolated from *Diplanthera*. See Figure 2 for operating conditions.

Table 2 gives the hydrocarbon composition of the five "grasses" tested. Each genus is distinct, but there are obvious groupings of them: the most obvious groupings of them: the most obvious segregate is *Ruppia*. The hydrocarbons of *Ruppia* are restricted to 23–31 carbons by this procedure; and the predominant

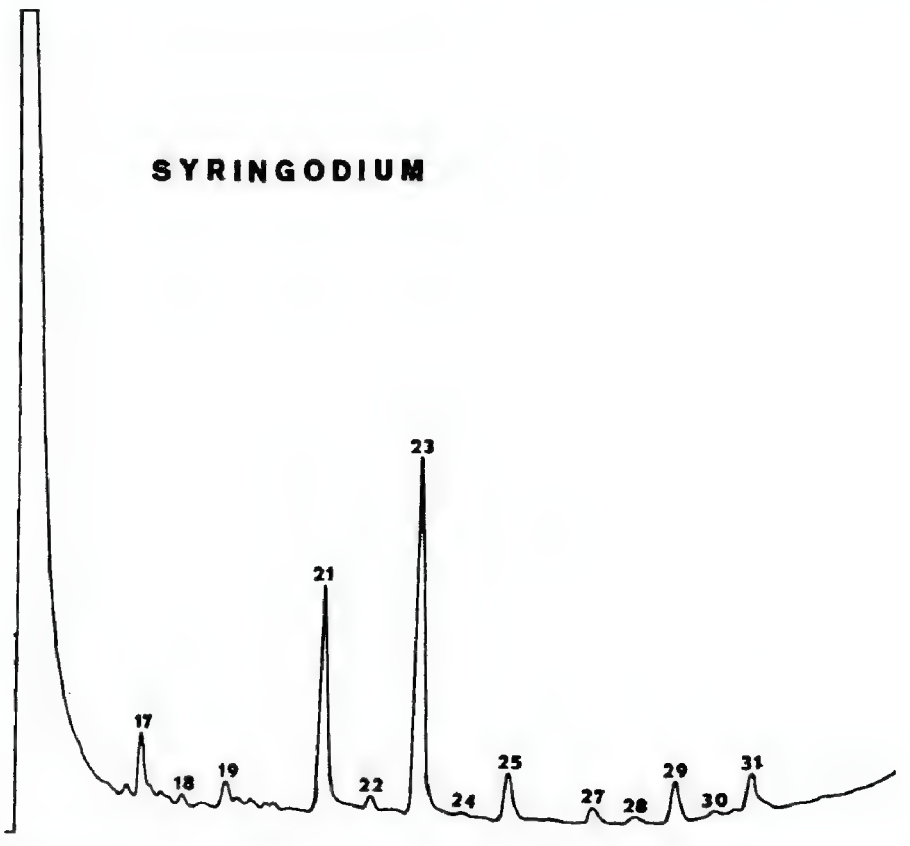

FIG. 4. Gas chromatogram of alkane fraction isolated from *Syringodium*. See Figure 2 for operating conditions.

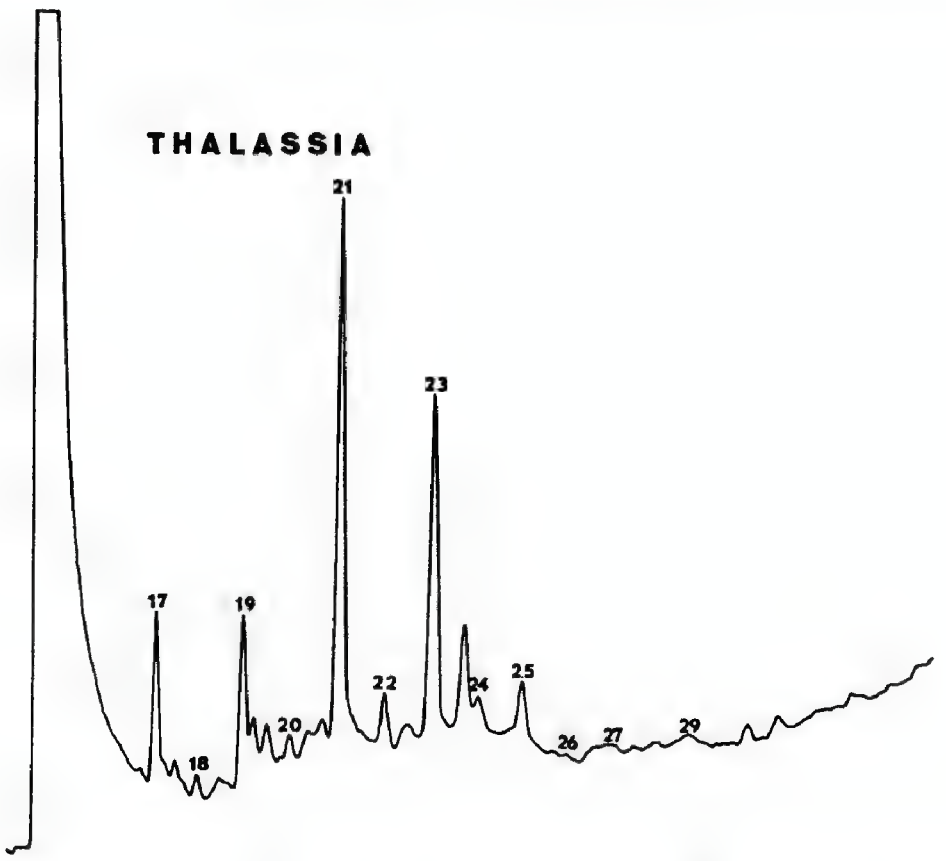

FIG. 5. Gas chromatogram of alkane fraction isolated from *Thalassia*. See Figure 2 for operating conditions.

component is a C_{27} hydrocarbon, the highest molecular weight of all the major peaks of "sea grasses." The other four genera are segregated into two groups. *Syringodium* and *Diplanthera* into one and *Halophila* and *Thalassia* into another.

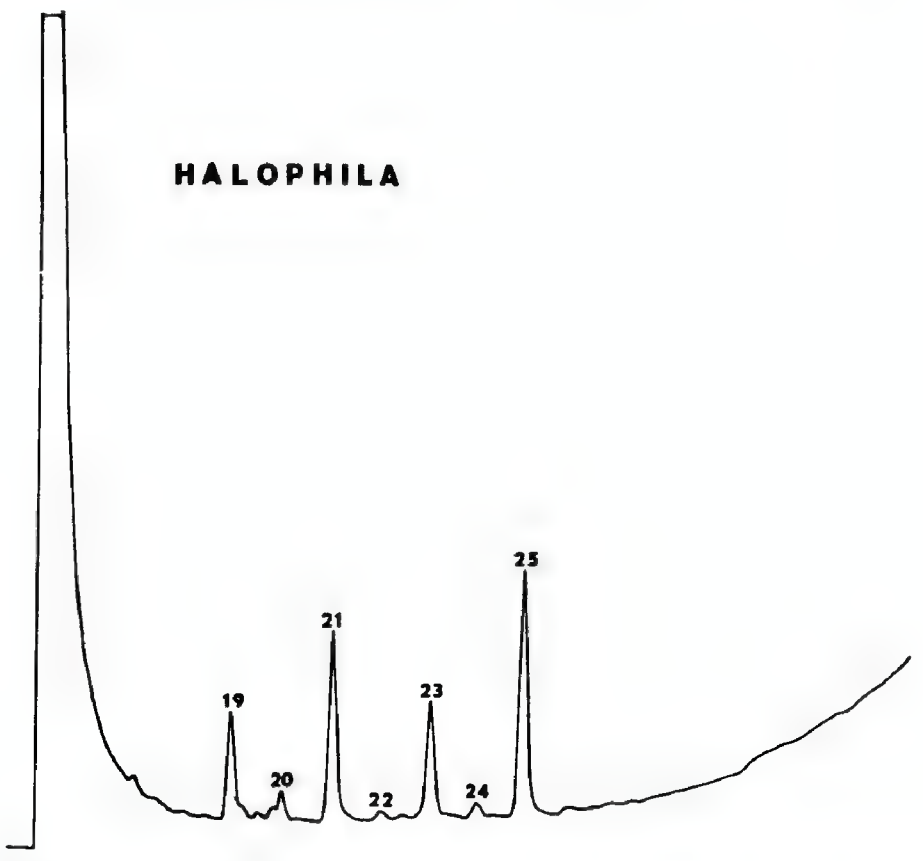

FIG. 6. Gas chromatogram of alkane fraction isolated from *Halophila*. See Figure 2 for operating conditions.

TABLE 2

Percent Composition of the Alkane Fractions
of Five Coastal Spermatophytes

Number of carbon atoms	Syringodium	Diplanthera	Genera Ruppia	Halophila	Thalassia
15	—	0.4	—	—	—
16	—	0.3	—	—	—
17	5.8	15.8	—	—	9.2
18	1.2	3.6	—	—	1.2
19	3.5	11.8	—	13.6	11.4
20	—	2.4	—	4.4	1.5
21	20.6	3.4	—	23.0	33.5
22	1.8	0.6	—	0.9	3.9
23	44.0	15.7	8.5	19.7	26.2
24	1.0	1.4	0.8	2.4	2.9
25	6.5	19.8	22.0	36.2	5.7
26	—	0.7	2.3	—	1.2
27	3.1	13.4	50.6	—	2.6
28	1.2	0.8	1.7	—	—
29	5.5	8.1	13.6	—	—
30	1.2	0.3	—	—	—
31	5.1	0.7	1.4	—	—
Average	23	23	27	23	21

The main distinction of these two groups is that the *Syringodium-Diplanthera* group has a broader range (particularly, higher) of hydrocarbons.

Within the three major groups some additional structure exists. *Halophila* and *Thalassia* have similar patterns: the 17, 18, 26 and 27 carbon peaks are not major; they share major peaks of 21 and 23 carbons, the main difference being *Halophila*'s very strong peak at C_{25}. While there are several similarities between *Thalassia* and *Halophila*, there is a major difference which can be expressed in terms of the average number of carbons in the hydrocarbons of each genus: 23 for *Halophila* and 21 for *Thalassia*. That difference is quite significant when it is observed that the absence of short chain hydrocarbons in *Ruppia* accounts for an average difference of only four carbons from the 23 carbon length which appears average in these measurements.

Syringodium and *Diplanthera* are more similar. While the C_{25} peak in *Syringodium* distinguishes it from *Diplanthera*, the ranges and average hydrocarbon lengths are very similar.

The groupings discussed above are shown in Figure 7. The segregation pattern

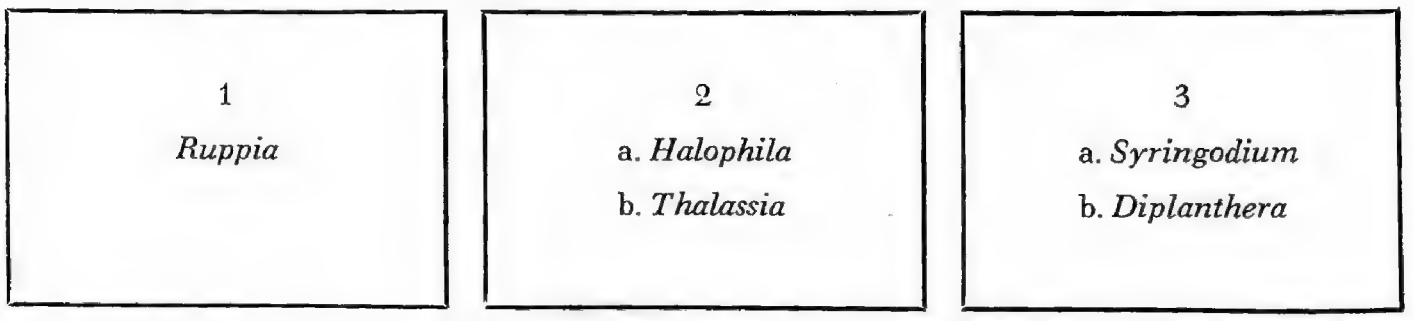

FIG. 7. Segregates of "Sea Grasses".

in Figure 3 corresponds with the modern taxonomy of the "grasses" (Hutchinson 1959, p. 541, 558–559) where (1) is the Ruppiaceae, (2) is the Zannicheliaceae and (3) is the Hydrocharitaceae (3a, the Halophiloideae and 3b the Thalassioideae). These data do not suggest distances of relation, so it is not clear how closely the families 1, 2, and 3 are related. Unpublished data of Attaway, Haug and Parker on the distribution of sterols in these plants also support the classification system of Hutchinson.

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SIZE OF PINFISH IN RELATION TO THERMAL STRESS RESPONSE

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ABSTRACT

At temperature ranges of 10–20 C and 20–30 C, respiratory rates were determined for groups of four fish, each selected into large and small size ranges. Oxygen consumption rates determined by use of a rotating chamber were analyzed by multiple regressions relating the log oxygen consumption rate to log weight, temperature and swimming velocity. Multiple, partial and simple correlations among these variables also were calculated. All calculations were for small, large and combined size ranges.

Analyses for combined size groupings yielded partial regression coefficients in agreement with data previously published. Definite differences exist in regressions for small and large groups when calculated separately at the two temperature ranges: at the 10–20 C range the respiratory-weight coefficients are unusually low for both large and small groups; at the 20–30 C range the coefficient for only the large fish is low.

Calculated oxygen consumption rates on a unit weight basis for small, large and combined sizes at zero activity and over each of the temperature ranges revealed inconsistencies. At 20–30 C the calculated oxygen consumption rates per unit weight for small fish were, as expected, above the rates for the large fish; at 10–20 C the calculated rates were disproportionately high for the large fish compared to the rates for the small fish. Among the simple and partial correlations relating oxygen consumption to weight, pronounced discrepancies between small fish (positive correlations) and large fish (negative correlations) occur only at the lower temperature range.

The disproportionate differences in metabolism and the discrepancies among the correlations of oxygen consumption rates only at lower temperatures suggest strongly that there is an interaction among respiration, weight and temperature.

INTRODUCTION

This study was designed to evaluate the effects of temperature on fish of different sizes. Wohlschlag *et al.* (1968) have indicated that the pinfish, *Lagodon rhomboides*, at a 10–20 C range has oxygen consumption on temperature regressions that appear to be different from the 20–30 C regressions, when compared to the oxygen consumption rates per unit weight actually observed; the latter regressions agree with observations, while the former do not. Similarly, Wohlschlag and Cameron (1967) have shown that a sublethal pollution stress over a broad thermal range has a relatively uniform effect of depressing respiration for

smaller fish, while the larger fish experience a relatively greater respiratory depression at upper and lower temperatures.

From a geographical standpoint, it is commonly recognized that environments with high thermal extremes have fewer and smaller fish species, although the environments with low temperature extremes regularly have larger fishes (Lindsey 1966). The considerable literature on effects of temperature on metabolism of poikilotherms generally does not provide identifications of specific mechanisms whereby temperature would have a differential metabolic effect in terms of size.

From the standpoint of growth theory, Ursin's (1967) extensive review would indicate that energy requirements for maintenance increase relative to growth requirements to the extent that the rate of change of weight tends toward zero with age and size and that theoretically there would be little energy available for larger fish to cope with stresses of thermal or other origins. That larger fish cannot cope with cold shock is widely known along the coast of the Gulf of Mexico; pertinent publications on this phenomenon are summarized by Wohlschlag *et al.* (1968). That the larger pinfish (and other fishes) tend to move off Gulf coast "grass flats" during diurnal and seasonal high temperature extremes, while the smaller fishes tend to remain longer, is discussed by Cameron (1969).

To elucidate the temperature-size effects, an experiment was set up over a wide range of temperatures to determine the relative respiratory rates of pinfish selected artificially into small and large size ranges.

METHODS

Techniques used in this study follow closely those used by Wohlschlag and Juliano (1959), Wohlschlag and Cameron (1967) and Wohlschlag *et al.* (1968).

Pinfish from the Aransas Pass at the pier laboratory (27° 50′ N, 97° 03′ W) provided the experimental animals used from April through June. Salinity of the pass varied from 32 to 34 ppt depending on tidal flows. Initial acclimation of the fish was by means of retention in a large, thermally controlled and aerated aquarium to the 5 C interval nearest the ambient environmental temperature. After an initial period of two or three days, there were either respiratory measurements or a change to the adjacent and approximate 5 C interval, after which either a further two-day acclimation period ensued at 25 and 30 C or a three-day period ensued at 10, 15 and 20 C. This procedure was continued until experiments were conducted at approximately 10, 15, 20, 25 and 30 C. Temperature control was to about ± 0.05 C.

At each of these temperature ranges, respiratory rates were determined for groups of four fish of similar sizes; each group was selectively made up of "small" or "large" specimens which were held in the aquarium together.

Oxygen consumption rates of these groups were calculated from dissolved oxygen content measurements in four successive 15-min intervals for samples of the confined water of a metabolism chamber. Dissolved oxygen values were determined by the azide modification of the Winkler method. The 42,140 ml chamber consisted of a circular clear plastic enclosure, which could be rotated. The average swimming "track" was 2 m per revolution; rotational velocity control was by means of a rheostat and a constant-torque motor mechanism, which was attached to the chamber suspension system. The chamber was immersed in the 462-l temperature-controlled aquarium, which also served as the acclimation aquarium.

During each run the chamber was rotated at whatever velocity the group of four fish would swim consistently. Several times at each temperature level, blank runs (without fish) were made for the purpose of correcting for any oxygen consumption by small organisms or chemical systems in the water.

At the termination of runs the fish in the chamber were individually weighed, the temperature

and revolutions of the chamber recorded, and the rates of oxygen consumption calculated by a least squares regression after an appropriate correction for the blank run.

Computerized analysis of the data was by the multiple regression and correlation techniques as described in statistical manuals (e.g. Snedecor and Cochran, 1967). For each of the groups of small and large fish and for the combined data, the oxygen consumption rates may be related to the several independent variables in the form

$$Y = a + b_w X_w + b_t X_t + b_s X_s,$$

where

Y is the expected log mg 0_2 consumed per hour,

a is a constant

b_w is a partial regression coefficient of the increase in Y per unit increase in log weight at a constant temperature and swimming velocity,

X_w is the log weight in grams,

b_t is the partial regression coefficient of the increase in Y per degree increase in temperature at a constant weight and swimming velocity,

X_t is the temperature in C,

b_s is the partial regression coefficient of the increase in Y for each m/min increase in swimming velocity at a constant weight and temperature, and

X_s is the average swimming velocity in m/min.

Throughout, oxygen consumption and weight are on the basis of averages for the individuals in the groups of four fish.

Data in the 10–20 C range were analyzed for groups of 17 small, 19 large and 36 large and small fish combined; data in the 20–30 C range were analyzed for groups of 18 small, 19 large and 37 large and small fish combined. For each of the regression analyses, appropriate correlations and partial correlations were tabulated.

RESULTS AND DISCUSSION

A schedule of weight ranges and the average weight of the fish in each of the groups and in each of the temperature ranges is:

	10–20 C	20–30 C
Small:		
Sample size	17	18
Range	23.1–50.9 g	24.3–46.4 g
Mean	35.9 g	32.3 g
Large:		
Sample size	19	19
Range	67.1–130.9 g	56.4–128.2 g
Mean	85.8 g	82.2 g

Techniques

General critiques of the methods used in this study follow those for respiratory metabolism measurements reviewed by Wohlschlag *et al.* (1968) and will not be repeated here. Not coincidentally, the results of the multiple regression analyses for the combined respiration measurements for both large and small fish (Table 1) agree well with the multiple regressions for pinfish in late spring or summer (Wohlschlag *et al.* 1968). However, in the present study, the major exceptions to these regression statistics are primarily associated with the arbitrary subdivision of the respiratory rate relationships, which differ between large and small fish, even though both size ranges were acclimated simultaneously.

TABLE 1

Regression statistics for comparisons among large and small pinfish over two temperature ranges

		10–20 C			20–30 C		
		Small	Large	Large and small	Small	Large	Large and small
Multiple Regression	N	17	19	36	18	19	37
	R	0.96	0.92	0.95	0.71	0.86	0.93
	F	47.45**	21.15**	103.39**	4.65*	13.61**	75.79**
	s_Y	0.1006	0.1028	0.0991	0.0756	0.1068	0.0908
	x_w	1.556	1.934	1.755	1.509	1.914	1.717
Weight	b_w	0.4433	0.4615	0.7912	0.9151	0.5351	0.8812
	s_{b_w}	0.3303	0.4719	0.0815	0.3499	0.2942	0.0694
	"t"	1.34	0.98	9.71**	2.61*	1.82	12.70**
	x_t	15.36	15.20	15.28	25.55	25.21	25.38
Temperature	b_t	0.0365	0.0356	0.0375	0.0148	0.0212	0.0173
	s_{b_t}	0.0078	0.0079	0.0047	0.0065	0.0054	0.0031
	"t"	4.68**	4.51**	7.98**	2.28*	3.93**	5.58**
	x_s	8.45	8.00	8.21	9.83	10.65	10.25
Swimming Velocity	b_s	0.0366	0.0258	0.0296	0.0249	0.0279	0.0288
	s_{b_s}	0.0096	0.0086	0.0062	0.0093	0.0086	0.0059
	"t"	3.81**	3.00**	4.77**	2.68*	3.24**	4.88**
Intercept	a	—0.6658	—0.4531	—1.1562	—0.8556	—0.3254	—0.8979

* $0.01 < P < 0.05$
** $P < 0.01$

The choice of groups of four fish is arbitrary. In order to obtain respiration rates at the lowest possible level consistent with survival, the standard rates from large groups under darkened laboratory conditions (Wohlschlag *et al.* 1968) could not be obtained by using individual quiescent fishes or by extrapolating to zero swimming velocity from regressions based on respiration data from a series of individual fish swimming at different velocities. The extrapolation to zero velocities from pinfish data given by Wohlschlag *et al.* (1968) and Wohlschlag and Cameron (1967) are generally consistent with the data of Cameron (1969) who utilized quiescent fish in large flasks. Four individuals per respiration rate determination tended to have rates that were most nearly "standard" largely because the amount of "spontaneous" non-locomotor activity tended to be visibly absent when the four fish swam in groups than when single fish swam in the rotating chamber.

The choice of temperature ranges of about 10 C to 20 C and about 20 C to 30 C is likewise arbitrary. The use of a single curvilinear line over the 20 C range seems impracticable, because (1) no single metabolism-temperature function for the pinfish prevails through the year and (2) no simple biological significance can be attached to a series of constants calculated for higher order equations that "fit" the observations (Wohlschlag *et al.* 1968). By characterizing the relationships in terms of log O_2 consumption rate compared to temperature with two linear equations, each over an approximate 10 range, the observations are characterized reasonably well, and the constants derived for the regression co-

efficients agree well with published values, except for the major discrepancies discussed below.

One of the most obvious effects of the arbitrary size groupings is evident from a comparison of the respiration-weight coefficients (b_w) in Table 1. For the combined data the b_w are of the order of 0.8 which Winberg (1956) found to be average for a large number of fish species. For the restricted weight ranges at either temperature range only the small fish at the higher temperature range had a b_w at the "realistic" level; the other b_w for the size-restricted groups are all much lower. The b_w for pinfish generally tend to be at or above the 0.8 level (Wohlschlag and Cameron 1967; Wohlschlag *et al.* 1968; Cameron 1969). However, it is quite frequent that similar small values of b_w appear in the literature, although the explanations are not often straightforward for what might be termed aberrantly high or low values (Paloheimo and Dickie 1966).

One of the obvious explanations for unusually high or low respiratory-weight coefficients pertinent to groups of fish with small weight ranges would hinge on the degree of ordinary statistical variability among the measurements. With a narrow distribution of weights, it is possible that one or two relatively discrepant respiration rate measurements at either extreme of the narrow weight distribution would yield b_w either far above or far below a value of about 0.8.

A less obvious cause of low b_w values is explained by Glass (1969), who shows that the logarithmic transformation of respiration rate and body weight for a linear equation is correct only when the random error term itself is in logarithmic (multiplicative) form. Should the logarithmic transformation have an error term in arithmetic (additive) form, the use of the logarithmic transformation for calculating b_w would be invalid. However, in this study, the very low values of the b_w for some of the size-restricted groups of fish would not be raised too substantially by the iterative solutions of the respiration-weight equation suggested by Glass (1969); alternatively the data and general field observations would at least suggest that interactions of body size with temperature (or perhaps other environmental variables) might be more important than the simple consideration of random error terms as being additive.

In the following discussion, there are several precautions observed in the interpretations of the correlation data of Table 2. Aside from the possibilities of spurious or nonsense correlations there is the possibility that some statistical probabilities, which indicate "significant" correlations may arise by chance, even though all the variables measured were random and non-correlated. That significant correlations do exist between or among varaibles also is not necessarily indicative of causal relationships.

Temperature

The temperature coefficients agree with those for fishes in general and those for the pinfish published earlier. The increase in the coefficients with decreasing temperatures correspond to earlier data reviewed by Winberg (1956) and more recently by Precht (1968). By utilizing still lower temperatures near the lethal level, Cameron (1969) indicates that the high b_t values correspond to those in the range for thermal mortality.

TABLE 2

Simple, partial and multiple correlations for comparisons among large and small pinfish at two temperature ranges

Size range	10–20 C Small	10–20 C Large	10–20 C Combined	20–30 C Small	20–30 C Large	20–30 C Combined
Number	17	19	36	18	19	37
Simple Correlations:						
r_{Yw}	0.50*	—0.50*	0.47**	0.41	0.43	0.83**
r_{Yt}	0.90**	0.86**	0.75**	—0.16	0.70**	0.21
r_{Ys}	0.86**	0.76**	0.68**	0.50**	0.52*	0.43**
r_{wt}	0.41	—0.68**	—0.06	—0.80**	0.31	—0.12
r_{ws}	0.37	—0.37	—0.05	0.34	—0.01	0.20
r_{ts}	0.71**	0.60**	0.65**	—0.46	0.15	—0.11
Partial Correlations—Three Variables:						
$r_{Yw.t}$	0.33	0.24	0.79**	0.47*	0.31	0.88**
$r_{Yw.s}$	0.38	—0.36	0.69**	0.29	0.51*	0.84**
$r_{Yt.w}$	0.87**	0.82**	0.89**	0.30	0.66**	0.56**
$r_{Yt.s}$	0.80**	0.78**	0.56**	0.09	0.74**	0.29
$r_{Ys.w}$	0.84**	0.72**	0.80**	0.42	0.58*	0.48**
$r_{Ys.t}$	0.72**	0.61**	0.38*	0.48*	0.59**	0.47**
$r_{wt.s}$	0.22	—0.62**	—0.04	—0.78**	0.32	—0.10
$r_{ws.t}$	0.13	0.07	—0.01	—0.06	—0.06	0.19
$r_{ts.w}$	0.65**	0.51*	0.65**	—0.34	0.16	—0.09
$r_{wt.Y}$	—0.11	—0.57*	—0.72**	—0.82**	0.02	—0.54**
$r_{ws.Y}$	—0.13	0.02	—0.58**	0.17	—0.30	—0.31
$r_{ts.Y}$	—0.28	—0.18	0.28	—0.44	—0.36	—0.23
Partial Correlations—Four Variables:						
$r_{Yw.ts}$	0.35	0.24	0.86**	0.57*	0.43	0.91**
$r_{Yt.ws}$	0.79**	0.76**	0.82**	0.52*	0.71**	0.69**
$r_{Ys.wt}$	0.72**	0.61**	0.65**	0.58*	0.64**	0.65**
$r_{wt.sY}$	—0.15	—0.58*	—0.72**	—0.84**	—0.10	—0.66**
$r_{ws.tY}$	—0.17	—0.10	—0.56**	—0.37	—0.31	—0.53**
$r_{ts.wY}$	—0.30	—0.20	—0.24	—0.54*	—0.37	—0.50**
Multiple Correlation:						
$R_{Y.wts}$	0.96**	0.92**	0.95**	0.71*	0.86**	0.93**

* $0.01 < P < 0.05$
** $P < 0.01$

Quite oddly, the weight-temperature simple and multiple correlations of Table 2 tend to indicate negative interrelations between temperature and weight, a situation which could arise if there were conscious selection of smaller fish at the higher temperature and *vice versa*. Because there was no evidence of this type of selection (inasmuch as both large and small fish were included in each range of thermal acclimation and in each series of respiration rate determinations) and because no physiological or ecological explanation appears evident at this time, it must be concluded tentatively either that these highly significant correlations arose by chance or that undetected selection of sizes within the various temperature levels can have important effects requiring further study, especially at temperature extremes.

Curvilinearity could have been introduced as a cause of the significance of some

of the weight-temperature correlations simply by the use of the log weight transformation. However, the use of the weight variable in log form is essential for relationships with oxygen consumption rates (also in log form) and is satisfactory in correlations and regressions for half the size-grouped data and for all the combined data.

Respiration-Weight Comparisons

By calculating the oxygen consumption rates on a unit weight basis, the differences between the large and small fish at the two temperature ranges are obvious as illustrated in Figure 1. In this figure are the calculated oxygen consumption rates per kilogram at zero swimming velocity for the average weights or both small and large fish combined (dashed lines) and for the average weights of each

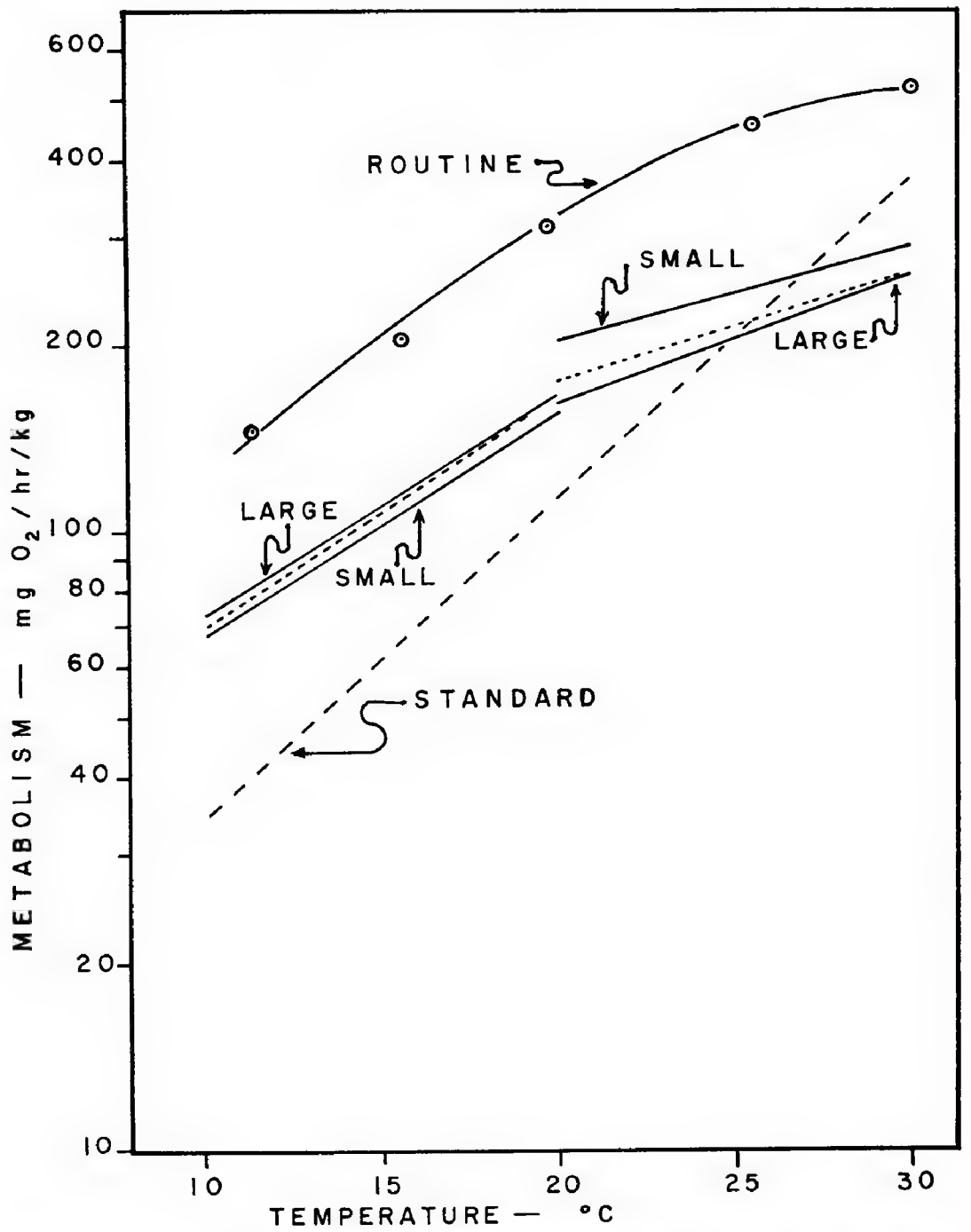

FIG. 1. Calculated oxygen consumption rates per kilogram for pinfish over two temperature ranges. Calculations are for small, large and combined size groupings at zero swimming velocity. Data on routine and standard rates from Wohlschlag *et al.* (1968).

of the small and large groups; in the same figure are the routine and "standard" rates from Wohlschlag *et al.* (1968) for fish at about the same time of the year. The combined data at both temperature ranges and at zero velocity tend to parallel the curve for the routine data and are generally coincident at the 20 C level. Strikingly, the large fish at the lower temperature range have greater, and not lesser, rates than would be expected, as is the case in the higher temperature range. Also the lines for large fish are more or less coincident at the 20 C level, while the lines for the small fish are not. Why both the large and small fish at 10–20 C have oxygen consumption levels (on a weight adjusted basis) above the "standard" levels (determined for much larger groups under darkened conditions) is not exactly clear; whether the higher rates imply metabolic loading, especially for the larger fish, is a possibility at lower temperatures, although it might be pointed out that the "standard" line at the lower temperatures may itself be depressed due to inhibition of metabolism under darkened conditions (Brett 1957, 1958). For fish corresponding to the smaller sizes in this study, Cameron (1969) notes that the temperature coefficient for winter temperature ranges is unusually high ($Q_{10} = 22$), resembling lethal ranges for thermal death (Giese 1962). With indications in Figure 1 of very high respiratory metabolism at lower temperatures for the small fish, and even relatively higher for the large fish, it is likely that loading can occur, even if the standard line were rotated clockwise to any reasonable degree. In this study, the period of thermal acclimation was only three days over five degree ranges at the lowest temperatures, while acclimatization over a much longer time at these temperatures may well have resulted in eventual metabolic depression or death. It is generally accepted that at very low temperatures acclimatization time tends to be much longer than at ambient temperatures. It is not known at present just how long and to what magnitude loading can persist without deleterious physiological impairment at various sizes and temperature extremes.

At the upper temperature range, the fact that the respiratory levels fall below the "standard" indicates that the larger fish especially suffer the greater depression of respiratory metabolism. Cameron (1969) also shows conclusively that metabolic depression at 31.7 C is definitely below the summer trend at a range of about 25–30 C.

The effects of stresses, including thermal extremes, on many aspects of fish behavior are often about the same as the effects of anesthesia. McFarland (1959), among others, notes that anesthesia has an influence that is greater the larger the fish; he notes that the mechanism of increased susceptibility of larger fishes is not known, but that temperature exerts a major influence.

A review of the oxygen consumption rates, as correlated with weights or as partially correlated with either or both temperature and swimming variables, may be instructive. In Table 3 are some of the more pertinent correlations, which may be useful in identifying the existence of respiration-weight-temperature interactions. First of all the four tabulated correlations for both large and small fish combined yield values that may be expected for the various pertinent regression statistics in Table 1 or from earlier published regressions (Wohlschlag and Cameron 1967; Wohlschlag *et al.* 1968; Cameron 1969). While the regressions

TABLE 3

Simple correlations between oxygen consumption rates and weight and partial correlations in relation to temperature and swimming velocity of the pinfish for two temperature ranges and for small, large and combined weight groupings

	10–20 C			20–30 C		
	Small	Large	Both	Small	Large	Both
r_{Yw}	0.50*	—0.50*	0.47**	0.41	0.43	0.83**
$r_{Yw.t}$	0.33	0.24	0.79**	0.47*	0.31	0.88**
$r_{Yw.s}$	0.38	—0.36	0.69**	0.29	0.51*	0.84**
$r_{Yw.ts}$	0.35	0.24	0.86**	0.57*	0.43	0.91**

* $0.01 < P < 0.05$
** $P < 0.01$

for the separated size groups are based on relatively small numbers, the outstanding difference in sign of the r_{Yw} between the small and the large fish at the 10–20 C range is of considerable interest because the equivalent simple regression of the two sizes combined is still positive as expected. Because of the wide regression difference between the large and the small fish at the lower temperatures, it is evident that there must be a wide scatter so that the other partial regressions are all small and of little statistical interest. Quite likely the fact that the 10–20 C regression line for the larger fish lies above the line for the small fish is involved in any explanation of the difference in sign for the simple r_{Yw}. These anomalous regressions and correlations provide evidence for the existence of an interaction among the variables of oxygen consumption rate, body size and temperature at lower temperatures.

Swimming Velocity

In Table 1, the results indicate that the pinfish swam somewhat faster at the higher temperature range, while there is a slight tendency for the fish to expend more energy to swim at lower temperatures (Wohlschlag 1962). The b_s coefficients correspond to earlier data. There appears to be no major difference in the b_s between the large and small fish within either temperature range. However, had the swimming velocities been calculated in body lengths per unit time, the swimming velocity relationships to respiration would have been higher for the smaller fish in accordance with the usual hydrodynamical considerations (see Osborne 1961). Maximum efficiency of swimming would appear to be between 20 C and 25 C (Wohlschlag *et al.* 1968), but it is quite likely that unusual minimum activity would ensue at thermal extremes below 10 C or above 30 C (Cameron 1969).

The simple and the partial multiple correlations (Table 2), in which respiration and swimming velocity appear to be uniformly positive, yield no obvious evidence of interactions over the weight and temperature ranges of the experiment.

CONCLUSIONS

Pinfish in groups of four selected into small or into large size ranges have pro-

nounced differences in respiratory metabolism within a 10–20 C range and between a 10–20 C range and a 20-30 C range.

When the two size groups are combined, the respiratory metabolism over 10–20 C and over 20–30 C ranges conforms to expected values without any unusual aberrancies. Partial regression coefficients calculated to relate oxygen consumption rates to body size, temperature and swimming velocity for the combined data are nearly the same as those previously published for the pinfish; the simple and partial correlations among these variables yield positive values as expected.

For both the large and the small fish at the 10–20 C range, the respiration-weight partial regression coefficients are unusually low with large standard errors. Among the simple and partial correlation coefficients for the separate sizes, statistically highly significant negative values of the respiration-weight relationships appear for the large fish at the low temperature range.

Calculated oxygen consumption rates from the regressions for the average weights of small and large fish and for both sizes combined on a unit weight basis, yield ordinary expectations (with a possible slightly clockwise rotation of the lines) for the three lines at the high temperature range, but only for the line based upon the combined sizes at the low temperature range. At the low temperature range the calculated line for the large fish is displaced upward.

The occurrence of statistically highly significant negative correlations of weight and temperature at both temperature ranges and for the individual size categories is inexplicable.

From an evaluation of the calculated oxygen consumption rates per unit weight for the two size ranges and the two temperature ranges and from an evaluation of the irregularities in the simple and partial correlations involving oxygen consumption rates, body size and temperature for the different size groups and temperature ranges, it is tentatively concluded that there is a definite size-temperature interaction that would possibly be unfavorable to the larger pinfish.

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DIURNAL VARIATIONS IN THE ACTIVITY AND METABOLISM OF THE ATLANTIC MIDSHIPMAN, *PORICHTHYS POROSISSIMUS*[1]

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ABSTRACT

Studies on the activity and respiration of the Atlantic midshipman, *Porichthys porosissimus* show that the fish exhibits a definite diurnal activity rhythm which is reflected by variations in its respiratory rate. The fish are significantly more active at night than in the day; nighttime respiration is about 1.5 times higher than the daytime rate. Furthermore this activity is characterized by two more or less consistent peaks in respiration occurring at approximately 2230 and 0400 hours.

The diurnal activity patterns are apparently of an exogenous nature, controlled by light intensity, but the existence of an underlying circadian rhythm is not ruled out. The findings of this study also support previous data obtained by other methods, on the activity of *P. porosissimus*.

INTRODUCTION

The purpose of this study was to investigate the character of diurnal variations in the respiratory metabolism of the Atlantic midshipman, *Porichthys porosissimus* (Valenciennes) and the relation of respiratory metabolism to the behavior and ecology of the species.

Ignorance of the existence of diurnal fluctuations in respiratory metabolism of any organism can become a problem when measurements taken at different times are compared. Diurnal variations must be accounted for in any study which utilizes an organism of marked periodic behavior or activity. Such variations may also be used for the study of activity patterns in behavioral and ecological studies.

The Atlantic midshipman is found in the estuarine and shallow coastal waters of the Atlantic Ocean from Virginia to Argentina. The biology and life history of the Atlantic midshipman and its Pacific relative *P. notatus* have been investigated by Lane (1967), Gilbert (1968) and Arora (1948). The special problem of its biolumenescence has been treated by Nicol (1957) and Crane (1965). These studies have shown that the midshipman exhibits a behavior pattern common to many benthic fishes, which burrow into the substrate during the day and come out only at night. This characteristic pattern and the sedentary nature of the

[1] Modified from part of a thesis submitted to the Graduate School of the University of Texas at Austin, in partial fulfillment of the requirements for the degree Master of Arts, January 1970.

fish make it a suitable subject for a study of respiratory metabolism, because it can be confined to a closed respiration chamber for long periods without becoming too disturbed.

Clausen (1933) was one of the first investigators to demonstrate diurnal fluctuations in the metabolic rate of fishes. Oya and Kimata (1938) showed that the carp exhibited a strong diurnal tendency in its metabolism, with daylight respiration being much higher than nighttime respiration.

Winberg (1956) has made a comprehensive review of the literature on diurnal fluctuattions in metabolic rates in fishes. He concludes that while some fish show definite patterns, others show either no pattern or such irregular patterns as to defy classification. These differences he attributes to activity (feeding) cycles. Woodhead (1966) has reviewed the more general topic of the effects of light on fishes, and includes much information on diurnal activity and circadian rhythms in fishes.

METHODS AND MATERIALS

Daily changes in respiratory rate were measured for 15 large and five small midshipmen (average weights 65 gms and 25 gms respectively) during the winter months of 1969. These changes were taken to indicate changes in activity since they could be correlated with activity changes observed using a second method.

Midshipmen are extremely sensitive to light at any wavelength. Lane (1967) found that even dim light in the far red or blue range caused the fish to remain inactive at night. Therefore a system of measuring activity which could be used in the dark was developed. Precautions were taken to work with quiescent fish either by allowing an adequate acclimation time or by making observations of the fish over a great enough period that the fish could recover between observations from the excitement caused by earlier observations.

Fish used in the experiments were captured by means of trawls in Aransas Bay and in the shallow Gulf of Mexico and by means of wire mesh fish-traps and a tide-trap (described by Lane 1967) located at the University of Texas Marine Science Institute at Port Aransas, Texas.

Following capture, the fish were kept in aerated sea water aquaria for at least two days before they were used in experiments. Temperature and salinity varied in the aquaria according to natural fluctuations and therefore a period for acclimation to these conditions was not necessary. No attempt was made to feed the fish. The water was changed about once a week.

The bottoms of the aquaria were covered with 5–8 cm of smooth aquarium gravel. Gravel was used instead of sand or mud because it was cleaner to work with and would not introduce any materials into the water which might interfere with the dissolved oxygen determinations. Lane (1967) found that the midshipman prefers soft (mud) bottoms to hard (sand) ones, but the presence of gravel in these experiments did not seem to hinder the fish in their burrowing activities.

Metabolism was measured in 2800 ml Fernbach flasks equipped with water inlet and outlet tubes and neoprene stoppers. The flasks, up to six at a time, were placed in an insulated wooden aquarium fitted with a light-tight lid (Fig. 1). The fish were placed in the flasks, which also contained a layer of gravel, and given six hours in which to become acclimated to the chambers. During this time sea water constantly flowed through the chambers.

The experiments lasted from 24 to 48 hours during which time the fish remained undisturbed in the chambers. At two-, three-, or four-hour intervals the flow of water through the chambers was stopped and the chambers sealed for a 30-minute period. Water samples taken at the beginning and end of this period were analyzed for dissolved oxygen by the Azide modification of the Winkler method (Carritt and Carpenter 1966). Data on temperature and salinity were taken at each sampling time (See Table 1).

An arbitrary Activity Index was determined by making observations at irregular intervals during the day and night. The observer entered the room in which the fish were kept and noted

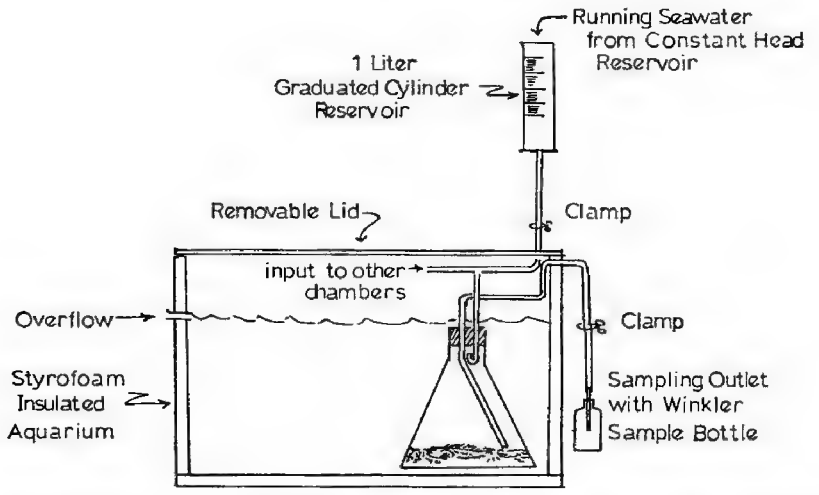

FIG. 1. General arrangement of metabolism chambers; up to six Fernbach chambers were placed inside the insulated aquarium.

the positions of each fish in the aquarium (there were six to twelve fish of different sizes in the aquarium at any time) and scored each fish according to the following system:

ACTIVITY SCALE

0 = fish buried
1 = fish resting on bottom
2 = fish swimming near bottom
3 = fish swimming more than 10 cm from bottom

This scale, in general, corresponds with the most common patterns of activity observed: resting on the bottom; slow swimming, just off the bottom; and rapid, darting movements carrying the fish upwards. This last catagory probably represents the type of movements commonly employed in prey capture.

TABLE 1

Experiment number	Duration (hrs)	Temperature (°C) Range	Mean	Salinity (‰) Range	Mean
024	32	16–18	16.6	27.3–32.4	29.6
025	32	16–18	16.6	27.3–32.4	29.6
026	32	15.5–17.7	16.5	26.8–30.6	27.9
027	32	15.5–17.7	16.5	26.8–30.6	27.9
028	27	16.3–17.3	16.7	28.8–32.8	29.8
029	27	16.3–17.3	16.7	28.8–32.8	29.8
031	34	13.9–15.5	14.5	20.7–29.0	24.6
032	34	13.9–15.5	14.5	20.7–29.0	24.6
034	25	12.8–14.0	13.4	26.8–27.3	27.0
035	25	12.8–14.0	13.4	26.8–27.3	27.0
036	25	12.8–14.0	13.4	26.8–27.3	27.0
037	25	12.8–14.0	13.4	26.8–27.3	27.0
038	24	17.5–18.5	16.8	20.9–29.0	24.1
039	24	17.5–18.5	16.8	20.9–29.0	24.1
040	24	17.5–18.5	16.8	20.9–29.0	24.1
041	24	17.5–18.5	16.8	20.9–29.0	24.1
043	24	15.5–18.5	16.8	29.0–31.0	30.2
045	24	15.5–18.5	16.8	29.0–31.0	30.2
047	48	17.5–21.0	19.2	31.2–33.0	32.6
048	48	17.5–21.0	19.2	31.2–33.0	32.6

The Activity Scale was multiplied by the number of fish in each state. These scores were then added together and the average Activity Index for the time period determined.

Example: data from 20:00, May 1, 1969

Scale	Number of Fish	Score
0	1	0
1	4	4
2	2	4
3	0	0
Sum of Scores		8
Total Number of fish		8

Activity Index = 8/8 = 1.0

To test the effect of burrowing on the metabolic rate of the midshipman, oxygen consumption was measured for five fish under each of the following conditions: nighttime. gravel in chamber; nighttime, no gravel; daytime, with gravel; and daytime, no gravel. Since the nighttime experiments were performed in the dark, and since it was assumed that the fish would be active during this time, the presence or absence of gravel should not make a difference. However, in the day a fish normally accustomed to burying was expected to be disturbed if burying was not permitted.

To examine the effects of constant illumination or constant darkness, three fish each were exposed to these conditions. The fish, in flasks with gravel, were acclimated for two days prior to the experimental period. Aerated sea water flowed through the chambers between oxygen consumption determinations.

RESULTS

The Activity Index experiments show that the fish are more active during the night. Since most of these observations were made during the spring, a time of lengthening light-periods, some of the observation times represent both light and dark conditions. In these cases the two points are differentiated; d = day and n = night. These data are illustrated in Figure 2.

Plots of metabolism (mg O_2/kg/hr) against time for two individual fish are given in Figure 3. These show that there are definite peaks of nighttime respiration. The mean value, range, and one standard deviation at each time period for the 20 experimental fish are shown in Figure 4. Note that the peaks, while still

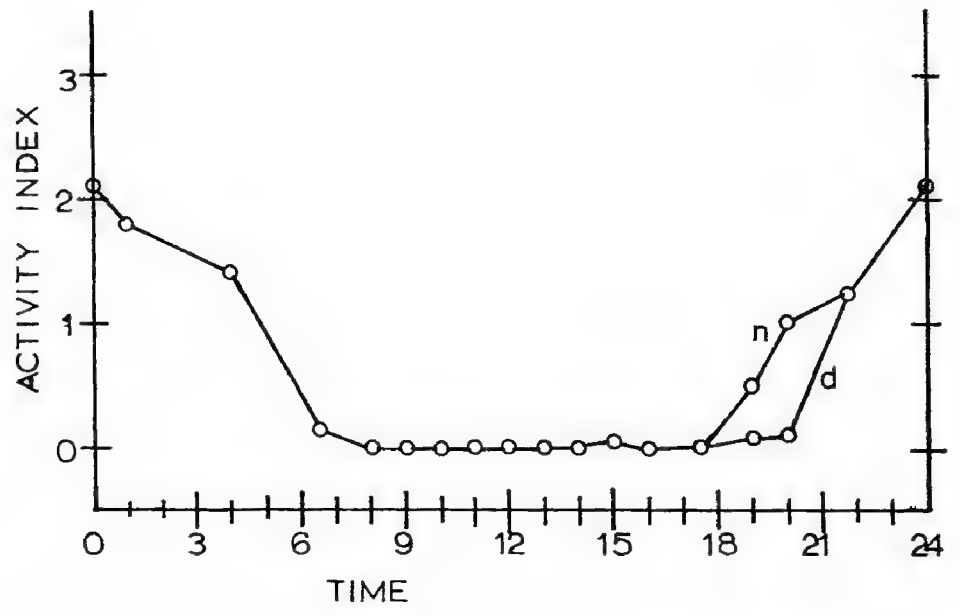

FIG. 2. Average activity levels for *Porichthys porosissimus* made over a two-month period. d and n differentiate observations made at the same time but under day or night conditions.

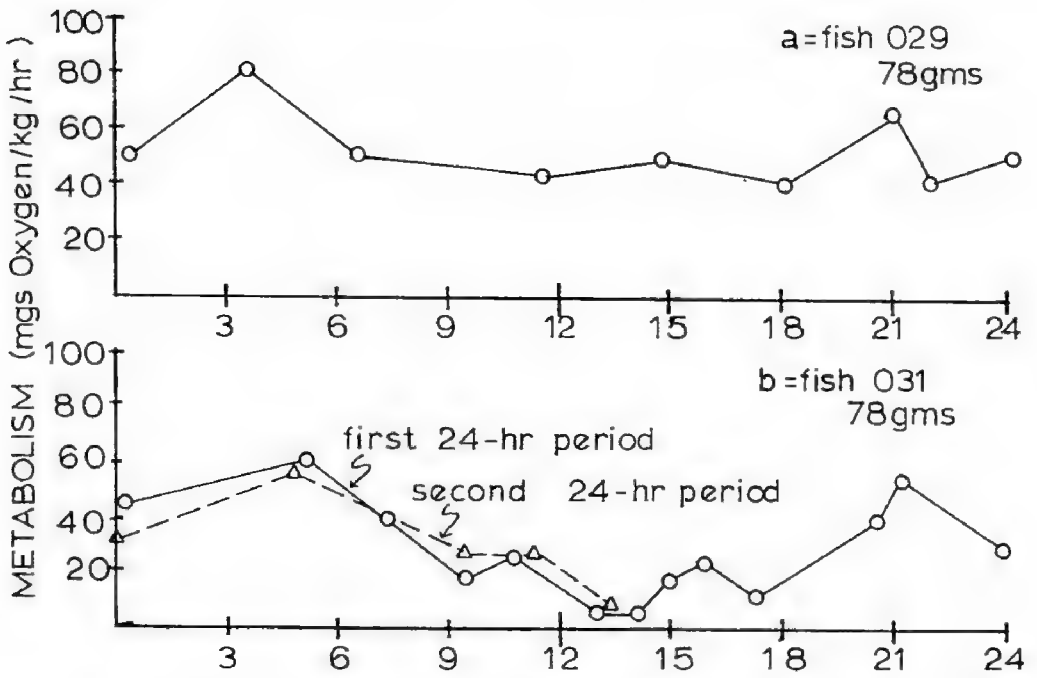

FIG. 3. Diurnal fluctuations in metabolism for two individual *Porichthys porosissimus*.

observable are less distinct. The ranges and means for temperatures and salinites during these 20 experiments are given in Table 1.

The average nighttime respiration (1800–0500) is significantly higher than the average daytime (0600–1700) rate as shown in Table 2. The results of a Student's-t test on paired day-night observations indicate a probability less than

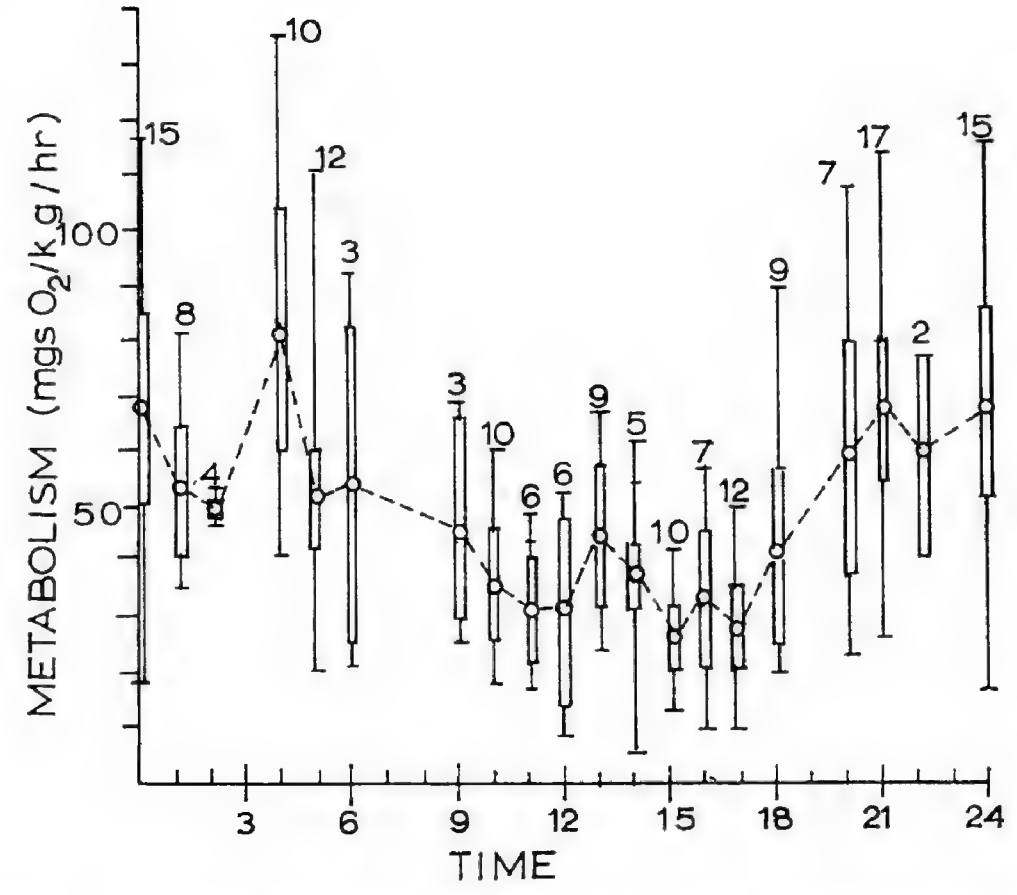

FIG. 4. Diurnal fluctuations in metabolism for 20 *Porichthys porosissimus*. The vertical bars represent the range of values at each time, the numbers above each of the bars represent the number of samples at each time, and the open bars represent one standard deviation about the mean metabolism value.

TABLE 2

Results of student's T-test on paired data for day (0600–1700) and night (1800–0500) metabolic rates for 20 midshipmen

Fish No.	Night rate	Day rate	Difference
024	103.32	63.43	39.89
025	103.33	83.33	20.00
027	31.18	33.96	—2.78
028	63.62	51.83	11.79
029	59.32	40.56	18.76
031	47.68	13.66	34.02
032	42.45	27.49	14.96
034	39.93	22.13	17.80
035	66.04	36.09	30.95
036	77.86	39.95	37.91
037	31.77	18.25	13.52
039	69.46	32.26	37.20
040	62.73	49.99	12.74
042	126.48	92.50	33.98
043	37.83	27.66	10.17
044	80.16	88.16	—8.00
045	108.27	47.52	60.75
046	119.78	105.98	13.80
048	151.36	75.69	75.67
049	123.92	100.63	23.29
Means	77.32	52.56	24.82=d

$t = 5.4681$ for 19 df $P < 0.0005$

TABLE 3

Data and results of a student's T-test on paired observations on midshipmen in the day and at night. Metabolism expressed in mgs O_2/kg/hr

Fish	Day			Night		
	With gravel	Without gravel	Difference	With gravel	Without gravel	Difference
A	10.4	33.7	23.3	68.5	66.7	—1.8
B	66.2	169.5	103.3	91.6	60.3	—31.3
C	82.1	100.5	18.4	75.6	65.5	—10.1
D	86.2	79.6	—7.0	113.2	121.1	8.5
E	12.1	56.8	44.7	103.6	74.8	—28.8
Sums	257.4	440.1	196.7	452.5	388.4	63.5
Means	51.1	88.0	39.3	90.5	77.7	12.7
Std. dev.	37.4	52.0	....	18.7	25.7	....

Results of daytime comparison:
$t = 2.2981$ for 4 df $0.05 < P < 0.10$

Results of nighttime comparison:
$t = 0.4761$ for 4 df $P > 0.60$

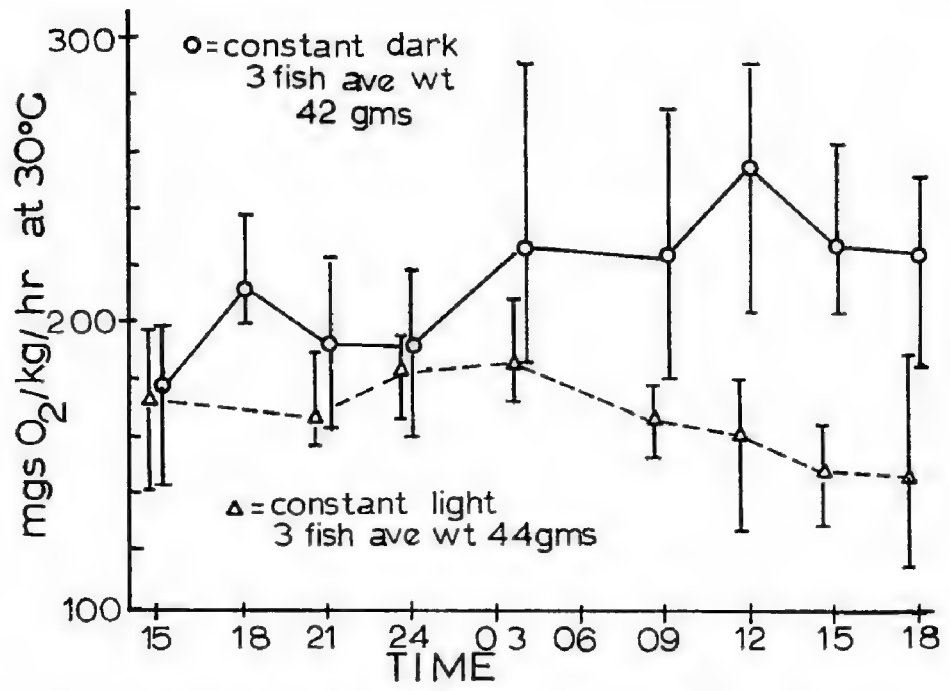

FIG. 5. Effect of constant light and dark on the metabolism of three midshipmen. The vertical bars represent the range of values at each time.

0.0005 ($t = 5.5$ for 19df) that there are no real differences between the average daytime and nighttime respiration.

The results of the time-substrate experimental combinations are shown in Table 3. While there are no statistically significant differences between the mean respiratory rates of buried and unburied fish at the two times there is a strong indication (as shown by the standard deviations) that in the day, fish not permitted to bury are more excited and have a greater variability in their metabolic rates. At night the results, as expected, are indistinguishable, the presence or absence of substrate makes little difference to the active fish.

The results of the time-substrate experimental combinations are shown in in Figure 5.

DISCUSSION

Many fishes have been shown to possess definite diurnal cycles in activity and metabolism. These cycles are usually associated with feeding regimes and are dependent upon environmental factors such as light, temperature and tidal rhythm which vary periodically.

Aschoff (1960) differentiates between exogenous and endogenous (circadian) rhythms. He states that if the periodicity is exogenous then the environment is the "real and only cause of the rhythm which ceases in artificial conditions."

Carlander and Cleary (1949), Spoor and Schloemer (1939), and Clausen (1936) have investigated activity cycles in freshwater fishes. The patterns of feeding activity which they found correspond well with the patterns in metabolic variation outlined by Winberg (1956).

Not as much work has been done on activity patterns in marine fishes, but studies have demonstrated that many reef-dwelling and benthic fishes exhibit some type of periodic activity (Verheijen and deGroot 1966; Kruuk 1963; Bardach *et al.* 1959; Livingston 1968). Hobson (1965) points out the importance of

such cycles in the ecology of reef-fishes. Activity cycles allow for more efficient resource sharing and thus reduce competition and at the same time can coordinate feeding or reproduction in a population.

Many benthic fishes are typically nocturnal. The nocturnal habit is easily understood as these fishes are often sluggish, inactive types. In the day they would be at a disadvantage in escaping predators and in catching prey. Therefore, many benthic fishes such as rays, flatfishes, and the midshipman remain buried or hidden in the day and emerges mainly at night.

The midshipman is known to be nocturnal in its feeding habits. Lane (1967) presents data to support this conclusion and suggest that the midshipman uses raptorial feeding methods at night when it is active. It is also capable of filter-feeding, a method which could be employed even while buried. My own observations (unpubl.) have confirmed both of these feeding methods.

The diurnal activity cycle of *Porichthys porosissimus* has been shown by variations in the metabolic rate as well as by observations of the fish themselves. The "Activity Index" by which the activity levels of the fish are presented is an imperfect system, but it allows a qualitative estimate of activity to be made.

The exogenous nature of the midshipman's activity cycle is demonstrated by the ease with which it adjusts to sudden changes in photoperiod. Fish which have been kept in the dark will burrow immediately if a light is turned on. Furthermore, when three fish were placed in a darkened aquarium at midday, all responded to the dark and within two hours were swimming about within the aquarium.

Lane (1967) performed experiments in which midshipmen were exposed to unnatural light cycles. Most of the fish responded within two days to the new cycles and thereafter remained "in phase".

The results of the constant illumination and constant darkness experiments also demonstrate the ease of adjustment of the midshipman to new light regimes. Under constant light conditions the midshipman retains a low metabolic rate throughout the experiment, indicating a low activity level. Neither were the fish seen above the gravel during this time. Under constant darkness the metabolic rates of the three fish fluctuated widely (see Table 4). These are probably indicative of periods of high and low activity. The average constant-dark values were approximately 1.2 times higher than the average constant-light values. This difference is significant as shown by the results of a t-test ($t = 18.27$, with 15 df, $P << 0.001$).

The overall increase in metabolic rate in the constant dark experiments, and the overall decrease in the constant light experiment may be indications that the fish had not *fully* adjusted to the new photoperiods and were becoming, respectively, more and less active as time passed (see Fig. 5).

The difference between the day and night activity levels in *Porichthys porosissimus* are quite marked as the "Activity Index" data shows. In the day the fish were seldom unburied, and in the night they were frequently swimming above the bottom. Although distinct peaks in nighttime activity are not discernable from these data, it is my opinion that they occurred. On the few occasions when more than one observation was made in an evening it was noted that different fish

TABLE 4

Results of the constant photoperiod experiments O_2 consumption in mg O_2/hr/kg

Time	Fish No.	Constant light conditions 143	144	145	Mean
1500		181.5	148.9	201.3	174.9
1800		....	....	....	....*
2100		165.2	162.8	195.8	174.6
2400		199.1	171.8	194.3	188.4
0400		178.3	185.9	212.2	192.1
0900		175.0	180.3	158.3	171.2
1200		183.6	131.9	170.6	162.0
1500		151.1	168.7	131.2	150.3
1800		193.3	140.1	119.4	150.9
Weight Fish		46 g	55 g	30 g	44 g
Time	Fish No.	Constant dark conditions 146	147	148	Mean
1500		182.0	199.2	143.6	177.3
1800		218.3	203.6	239.3	220.4
2100		221.8	163.9	198.7	194.9
2400		201.7	219.1	159.8	192.7
0400		278.3	206.3	183.4	222.6
0900		179.2	271.8	217.8	222.9
1200		260.1	201.6	288.2	249.9
1500		259.1	200.9	219.1	226.4
1800		208.8	248.7	183.5	213.7
Weight Fish		36 g	48 g	43 g	42 g

* Sample lost due to malfunction of equipment.

were in the more active states (2 and 3) at different times. In the averaged results these differences were obscured. To a lesser extent the same situation occurred in the oxygen consumption data where the individual peaks of activity are more clearly discernable in the respiration curves for single fish (Fig. 3) than in the curve for all fish (Fig. 4).

The only time in which a breakdown of the midshipman's diurnal habits under natural conditions was observed was in the fall of 1968 when captive fish spawned in the aquarium. At this time a large male remained active at all times, keeping other fish away from the nest-site and keeping the area adjacent to the nest clean (Moore 1970).

The existence of definite peaks in the nighttime respiration fits well with what is known of the feeding habits of the midshipman. The data indicates that there are periods of great activity followed by periods of reduced activity during which the fish presumably rests. During these times the metabolic rate is still higher than during the day, probably due to the increased energy demands from digestion, a higher rate of spontaneous activity, and the greater alertness of the fish.

The coordination of feeding activity among individuals is probably important ecologically; allowing all organisms to feed at approximately the same time, a factor which could be important since the time of feeding may be correlated with

the availability of prey-organisms, and at the same time slightly staggers the activity peaks, which may serve to reduce intraspecific competition.

The highest peaks of nighttime respiration occur at about 2230 and 0400. Two peaks occurred in most of the fish tested and all had at least one, most commonly the early morning peak. These peaks correspond with the peaks in activity and feeding intensity shown by Lane (1967) on the basis of catch-data and stomach-content analysis. Other fishes also have similar times of feeding (Livingston 1968; Verheijen and deGroot 1966; Kruuk 1963; Davis 1963).

SUMMARY AND CONCLUSIONS

The Atlantic midshipman, *Porichthys porosissimus* exhibits a definite diurnal activity cycles which is reflected by variations in its respiratory rate. During the day the fish remain buried in the substrate. The low energy demands of the fish during this time are shown by the low, fairly constant rate of oxygen consumption. During the night the fish, even while at rest, have a higher metabolic rate. At approximately 2230 and 0400 hours most of the fish tested showed definite peaks in nighttime respiration. These peaks correspond with the reported peaks in feeding intensity.

The importance of adequate knowledge of the activity rhythms of organisms used in studies on respiratory physiology is stressed, since ignorance of such periodic activity can cause errors in the comparison and interpretation of data.

The importance of such cycles to ecological studies are discussed with reference to temporal distributions as an important factor in niche separation.

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RELATIVE ABUNDANCE, SEASONAL DISTRIBUTION, AND SPECIES COMPOSITION OF DEMERSAL FISHES OFF LOUISIANA AND TEXAS, 1962–1964[1]

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ABSTRACT

Demersal fishes were collected monthly with a shrimp trawl at 33 to 60 stations in 7 to 110 m (4–60 fath) between the Mississippi River Delta and the United States-Mexico border from 1962 through 1964. Catches were generally two to five times greater off Louisiana than off Texas, with the greatest differences occurring in the shallowest waters.

Differences in total catches between stations within each depth off Texas and Louisiana, between day and night tows, and between years generally were not significant. Seasonal differences in catches were great off each coast.

The greatest catches off Louisiana were made in the winter and summer, and those off Texas were in the summer and fall. The largest catches were made between 7 and 46 m (4–25 fath) depths off Louisiana, and 27 and 110 m (15–60 fath) depths off Texas.

Atlantic croaker, *Micropogon undulatus* and longspine porgy, *Stenotomus caprinus*, constituted nearly half of the total catch. Atlantic croaker, longspine porgy, sand seatrout, *Cynoscion arenarius* and sea catfish, *Galeichthys felis*, were most abundant off Louisiana; longspine porgy, Atlantic croaker, inshore lizardfish, *Synodus foetens* and silver seatrout, *Cynoscion nothus*, dominated the catches off Texas.

INTRODUCTION

Before 1952, exploitation of many species of small demersal fishes was negligible in the northwestern Gulf of Mexico. Since then, however, a fishery for these species has developed in the north central Gulf. In 1967, this bottom trawl fishery caught 43,500 metric tons while an esitmated 590,000 metric tons were caught incidentally and discarded during shrimping operations (Bullis and Carpenter 1968). Today these fishes are processed only for animal food and fertilizer, but their potential value is even greater because of recent developments in the processing of fishes for human consumption as fish protein concentrate.

Several studies on the occurrence, abundance and distribution of demersal fishes on the Continental Shelf of the northwestern Gulf of Mexico were reported

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during the last 35 years. Investigations of the seasonal abundance of fishes were made in waters less than 27 m (15 fath) deep off Port Aransas, Texas (Gunter 1945; Miller 1965; Hoese *et al.* 1968) and Barataria Bay, Louisiana (Gunter 1936, 1938). The sampling by Gunter (1936, 1938, 1945), however, was in waters, never over, and usually much shallower than, 18 m (10 fath). In 1950–51, Hildebrand (1954) completed a general survey of fish abundance over the Continental Shelf in waters deeper than 27 m (15 fath) off Texas and Louisiana. However, no direct seasonal comparisons were attempted because samples were not taken throughout a year at the same stations and eleven different shrimp boats using trawls that ranged in width from 24 to 40 m (85–135 ft) were used in the study.

Distributions of fish species in the northwestern Gulf were listed in several reports (Springer and Bullis 1956; Hoese 1958; Bullis and Thompson 1965) and the size and species composition of the fish caught by the commercial fleet in the northern Gulf of Mexico were reported by Roithmayr (1965) and Gunter (1967).

The Soviet Union and Cuba jointly surveyed fish populations on the Continental Shelf of the northern Gulf of Mexico during four months in 1963–64 (Sal'nikov 1966). They trawled for concentrations of fish that had been detected with electronic gear. The sampling pattern was not reported but some general conclusions were made about the bathymetric distribution of fish concentrations. Sampling in these investigations over the last 35 years was not as extensive, or intensive, or both, as in our study.

In January 1962, personnel of the Bureau of Commercial Fisheries, Galveston, Texas, began a survey of fishes and crustaceans on the Continental Shelf in the northwestern Gulf of Mexico between the Mississippi River Delta and Brownsville, Texas. Stations were in depths between 14 m (7.5 fath) and 110 m (60 fath). Sampling continued through 1963 and 1964, but at a reduced number of stations between the 7 m (4 fath) and 73 m (40 fath) depth contours. Our sampling permitted the acquisition of data on seasonal, bathymetric, and areal distributions of demersal fishes. This information was analyzed: (1) to provide the fishing industry with information on the relative abundance and seasonal distribution of the demersal fishes caught (species combined) and (2) to denote species composition of the catches.

STUDY AREA AND SAMPLING METHODS

Sampling stations were established in the coastal waters of Louisiana and Texas along eight depth contours. Station locations, depth zones, and coastal regions are shown in Figure 1. The depth zones, determined arbitrarily, were: inner zone, 2–18 m (1–10 fath); middle zone, 20–55 m (11–30 fath); and outer zone, 57–110 mm (31 to 600 fath). Samples were collected during only one or two years at some stations. The location of each station and years of sampling are given in Table 1. Stations in the first column (W) were off Texas and stations in the second column (E) off Louisiana.

Samples were taken monthly from January 1962 through December 1964, with a 14-m (45-ft) wide, flat trawl fitted with rollers. The stretched mesh of the net was 6 cm (2.3 inches) throughout and the towing speed was about 3.0 knots. Tows were of about 1-hr duration and began on arrival at a station regardless of time of day. The amounts of fish caught from tows of longer or shorter duration were adjusted to catch per hour. Each tow was categorized as either

TABLE 1

Location, depth, and year of sampling at each station off the Texas and Louisiana coast, 1962 through 1964

Station (W.)	Latitude (North)	Longitude (West)	Depth		Years sampled			Station (E.)	Latitude (North)	Longitude (West)	Depth		Years sampled		
			M.	Fm.	1962	1963	1964				M.	Fm.	1962	1963	1964
1	29° 01′	95° 05′	14	7.5	X	X	X	1	29° 22′	93° 20′	14	7.5	X	X	X
2	28° 40′	94° 56′	27	15	X	X	X	2	28° 46′	93° 20′	27	15	X	X	X
3	28° 18′	94° 46′	46	25	X	X	X	3	28° 28′	93° 20′	46	25	X	X	X
4	28° 05′	94° 41′	64	35	X	.	.	4	28° 11′	93° 20′	64	35	X	.	.
5	27° 58′	94° 38′	82	45	X	.	.	5	28° 06′	93° 20′	82	45	X	.	.
6	27° 55′	94° 36′	110	60	X	X	.	6	27° 59′	93° 20′	110	60	X	.	.
7	27° 44′	95° 30′	110	60	X	.	.	7	28° 02′	92° 25′	110	60	X	.	.
8	27° 49′	95° 32′	82	45	X	.	.	8	28° 10′	92° 25′	82	45	X	.	.
9	27° 54′	95° 35′	64	35	X	.	.	9	28° 16′	92° 25′	64	35	X	.	.
10	28° 04′	95° 40′	46	25	X	.	.	10	28° 32′	92° 25′	46	25	X	X	X
11	28° 17′	95° 46′	27	15	X	.	.	11	28° 55′	92° 25′	27	15	X	X	X
12	28° 34′	95° 55′	14	7.5	X	.	.	12	29° 12′	92° 25′	14	7.5	X	X	X
13	28° 02′	96° 46′	14	7.5	X	.	.	13	28° 55′	91° 30′	14	7.5	X	.	.
13a	28° 19′	96° 21′	14	7.5	.	X	X	14	28° 40′	91° 30′	27	15	X	.	.
14	27° 54′	96° 37′	27	15	X	.	.	15	28° 29′	91° 30′	46	25	X	.	.
14a	28° 07′	96° 14′	27	15	.	X	X	16	28° 20′	91° 30′	64	35	X	.	.
15	27° 47′	96° 30′	46	25	X	.	.	17	28° 11′	91° 30′	82	45	X	.	.
15a	27° 57′	96° 07′	46	25	.	X	X	18	28° 06′	91° 30′	110	60	X	.	.
16	27° 41′	96° 23′	64	35	X	.	.	19	28° 00′	90° 35′	110	60	X	.	.
17	27° 37′	96° 20′	82	45	X	.	.	20	28° 12′	90° 35′	82	45	X	.	.
18	27° 32′	96° 14′	110	60	X	.	.	21	28° 16′	90° 35′	64	35	X	.	.
19	27° 01′	96° 32′	110	60	X	.	.	22	28° 23′	90° 35′	46	25	X	X	X
20	27° 04′	96° 42′	82	45	X	.	.	23	28° 34′	90° 35′	27	15	X	X	X
21	27° 06′	96° 48′	64	35	X	.	.	24	28° 54′	90° 35′	14	7.5	X	X	X
22	27° 08′	96° 56′	46	25	X	.	.	25	29° 10′	89° 42′	14	7.5	X	X	X
22a	27° 21′	96° 50′	46	25	.	X	X	26	29° 05′	89° 42′	27	15	X	X	X
23	27° 12′	97° 08′	27	15	X	.	.	27	28° 59′	89° 42′	46	25	X	X	X

TABLE 1—Continued

Location, depth, and year of sampling at each station off the Texas and Louisiana coast, 1962 through 1964

Station (W.)	Latitude (North)	Longitude (West)	Depth		Years sampled			Station (E.)	Latitude (North)	Longitude (West)	Depth		Years sampled		
			M.	Fm.	1962	1963	1964				M.	Fm.	1962	1963	1964
23a	27° 36′	96° 55′	27	15	.	X	X	28	28° 51′	89° 42′	64	35	X	.	.
24	27° 15′	97° 19′	14	7.5	X	.	.	29	28° 45′	89° 42′	82	45	X	.	.
24a	27° 48′	97° 00′	14	7.5	.	X	X	30	28° 40′	89° 42′	110	60	X	.	.
25	26° 14′	97° 08′	14	7.5	X	.	.	43	28° 48′	89° 42′	73	40	.	X	.
26	26° 15′	97° 00′	27	15	X	.	.	44	29° 15′	89° 42′	7	4	.	X	X
27	26° 21′	96° 41′	46	25	X	.	.	45	29° 01′	90° 35′	7	4	.	X	X
28	26° 24′	96° 31′	64	35	X	.	.	46	28° 13′	90° 35′	73	40	.	X	X
29	26° 25′	96° 26′	82	45	X	.	.	49	29° 29′	92° 25′	7	4	.	X	X
30	26° 26′	96° 21′	110	60	X	.	.	50	28° 10′	92° 25′	73	40	.	X	.
53	29° 19′	94° 41′	7	4	.	X	X	51	28° 09′	93° 20′	73	40	.	X	.
54	28° 00′	94° 38′	73	40	.	X	X	52	29° 42′	93° 18′	7	4	.	X	X
55	29° 03′	95° 06′	7	4	.	X	X								
56	28° 23′	96° 20′	7	4	.	X	X								
57	27° 46′	96° 00′	73	40	.	X	.								
58	27° 06′	96° 45′	73	40	.	X	.								
59	27° 51′	97° 01′	7	4	.	X	X								
60	26° 34′	97° 16′	7	4	.	X	X								
62	26° 41′	96° 53′	46	25	.	X	X								

day or night, depending on whether the longest duration of towing time was during the day or night. Day was defined as extending from 30 minutes before sunrise to 30 min after sunset.

Each catch was emptied on deck and the invertebrates were removed. Total volume of the fish caught was determined by measuring with containers of known volume. The total catch was estimated to the nearest 2.3 kg (5 lb.) by multiplying weight per unit volume by the total volume of fish in the sample. A random subsample of 1.8 kg (4 lb.) in 1962 and 3.5 kg (8 lb.) in 1963–64 was taken from most catches to determine average weight and relative abundance of each species.

Subsamples, preserved by freezing in 1962 and by formalin in 1963–64, were subsequently processed at the laboratory. Total weight of each species in a subsample was recorded to the nearest 5 g (0.2 oz). Species composition was estimated by dividing the species weight in the subsample by the total weight of the subsample.

Throughout this paper, the terms, "catch," "concentration" and "abundance" refer to the weight of fish caught per hour. Most fish caught were demersal, but some pelagic species were caught and are included.

ABUNDANCE

Total catches by station, month and year are shown in Table 2. We analyzed these data to determine the differences in catch between: (1) Louisiana and Texas waters, (2) day and night tows, (3) years and (4) seasons and depth zones.

Differences Between Coastal Regions

Annual mean catch by depth and year for each coastal region is shown in Table 3. The data upon which the means are based, and on which t-tests were run, represent those stations and months within a depth contour and coastal region at which samples were taken during a particular year (Table 2). Variability because of season, time of day, and between stations within a depth and coastal region was ignored in the comparisons. Nevertheless, the mean catch at depths out

TABLE 3

Comparisons of mean annual catch between Texas and Louisiana within each depth contour and year, 1962 through 1964

Year	Depth		Average catch (pounds/hour)		Test results	
	M.	Fm.	Texas	Louisiana	d.f.	t
1962	14	7.5	68	379	103	4.30[1]
	27	15	64	307	107	5.87[1]
	46	25	109	223	113	3.92[1]
	64	35	101	184	108	2.63[1]
	82	45	103	123	106	1.14
	110	60	89	81	98	0.73
1963	7	4	52	131	89	3.88[1]
	14	7.5	67	221	78	2.41[2]
	27	15	75	271	80	2.90[1]
	46	25	76	219	87	4.54[1]
	73	40	89	121	76	1.65
1964	7	4	62	137	99	2.58[2]
	14	7.5	72	271	73	1.99[2]
	27	15	58	229	81	4.12[1]
	46	25	74	168	74	3.57[1]

[1] Significance level = 1 percent.
[2] Significance level = 5 percent.

TABLE 2

Catch in pounds[1] per hour of demersal fishes (species combined) by year, station, depth, transect, and month from Texas and Louisiana, 1962–64

(Night catches are in italics)

Year	Station	Depth		Transect number	Month											
		M.	Fm.		January	February	March	April	May	June	July	August	September	October	November	December
1962	W-25	14	7.5	1	25	15	20	*210*	..	6	*4*	25	*250*	*5*	150	35
	W-24			2	25	*15*	10	120	*30*	*50*	20	*25*	..	30	*210*	*200*
	W-13			3	*20*	40	*10*	*20*	35	3	*200*	*300*	*40*	*90*	*65*	35
	W-12			4	14	..	30	65	*15*	10	..	125	*75*	40	100	..
	W-1			5	14	3	50	150	80	30	50	*60*	150	*225*	*50*	70
	E-1	14	7.5	6	45	335	*35*	*50*	45	35	60	200	*1,000*	..	..	..
	E-12			7	40	100	*150*	*50*	*200*	*4*	*250*	75	60	..	..	..
	E-13			8	*50*	*85*	160	40	450	30	2,500	300	300	..	525	..
	E-24			9	300	225	300	*1,600*	50	8	20	650	*1,250*	923	95	*1,600*
	E-25			10	*450*	275	*300*	1,200	25	*200*	*300*	300	1,500	..	*125*	..
	W-26	27	15	1	*25*	50	*25*	*25*	..	30	*20*	35	*70*	200	200	125
	W-23			2	15	*15*	20	30	..	10	48	20	50	300	200	*135*
	W-14			3	25	25	*50*	*50*	..	15	*15*	*40*	40	*35*	*75*	150
	W-11			4	15	..	50	15	30	20	..	50	86	70	150	55
	W-2			5	55	*30*	300	*25*	*15*	*30*	..	40	*25*	*35*	*70*	*100*
	E-2	27	15	6	*165*	150	200	*90*	20	*320*	*375*	*350*	*350*	*250*	200	*122*
	E-11			7	150	125	*105*	135	*80*	45	*70*	150	800	550	..	..
	E-14			8	*600*	*325*	*70*	20	60	*105*	75	*50*	200	*250*	*265*	525
	E-23			9	300	400	1,000	*900*	*35*	65	*1,000*	..	*500*	..	350	*350*
	E-26			10	*75*	220	*250*	750	175	*65*	*70*	500	850	..	*300*	1,400
	W-27	46	25	1	*60*	60	*350*	105	..	10	*15*	23	92	100	500	452
	W-22			2	*50*	*60*	*20*	50	..	6	93	6	120	65	20	125
	W-15			3	50	*100*	20	140	..	10	65	15	40	30	175	*70*
	W-10			4	80	80	*125*	80	*85*	50	150	225	40	50	45	120
	W-3			5	*150*	*200*	150	*60*	150	*100*	..	200	*90*	300	*150*	*300*
	E-3	46	25	6	*220*	225	180	90	150	200	125	*200*	451	650	145	*175*
	E-10			7	*356*	*100*	210	120	300	115	*250*	45	*700*	500	165	170
	E-15			8	*350*	*170*	*150*	42	300	*75*	125	*50*	60	*300*	*285*	900
	E-22			9	150	125	*600*	*75*	*50*	*35*	350	49	*40*	60	*96*	*700*
	E-27			10	*600*	220	*220*	70	375	*75*	*50*	90	25	..	*275*	131
	W-28	64	35	1	..	*75*	*80*	140	..	100	60	20	102	*150*	*175*	*200*
	W-21			2	55	50	80	40	..	*50*	*69*	4	50	*50*	130	250

TABLE 2—Continued

Catch in pounds[1] per hour of demersal fishes (species combined) by year, station, depth, transect, and month from Texas and Louisiana, 1962–64

(Night catches are in italics)

Year	Station	Depth		Transect number	Month											
		M.	Fm.		January	February	March	April	May	June	July	August	September	October	November	December
1962	W-16			3	85	*80*	25	120	..	50	70	80	30	50	100	*300*
	W-9			4	*95*	110	150	*135*	*70*	*150*	*200*	*75*	65	*100*	40	150
	W-4			5	*120*	90	*50*	80	*150*	40	165	..	60	300	130	*120*
	E-4	64	35	6	200	*150*	350	55	*100*	500	100	150	*75*	60	110	110
	E-9			7	*300*	150	*75*	44	..	30	50	*75*	*300*	60	800	..
	E-16			8	195	*85*	*175*	20	5	280	1,000	..	*40*	200	*253*	*165*
	E-21			9	150	20	*100*	37	*75*	*250*	200	*100*	105	*150*	*175*	1,200
	E-28			10	225	150	*210*	*85*	*40*	*20*	..	*15*	*40*	..	*250*	250
	W-29	82	45	1	..	*100*	*180*	200	..	50	..	100	80	*125*	*120*	100
	W-20			2	*85*	*75*	100	65	..	85	*65*	30	60	*8*	*150*	150
	W-17			3	45	*150*	*100*	25	..	*70*	70	*80*	105	300	110	..
	W-8			4	*100*	20	150	*70*	50	*76*	*210*	100	*25*	*240*	*55*	*180*
	W-5			5	*100*	80	*80*	..	*80*	150	50	130	*75*	200	160	..
	E-5	82	45	6	40	200	150	70	*85*	120	105	*75*	*150*	60	*40*	225
	E-8			7	*100*	..	175	33	35	*18*	100	*30*	*25*	*600*	19	*146*
	E-17			8	100	*260*	*100*	*80*	*200*	220	*200*	..	*100*	225	35	*150*
	E-20			9	*200*	*160*	*300*	20	175	*60*	500	*140*	70	*170*	*53*	100
	E-29			10	180	70	*20*	*45*	*30*	..	150	*20*	40	..	*48*	45
	W-30	110	60	1	..	*95*	50	100	..	..	..	..	110	*75*	*100*	200
	W-19			2	*50*	25	*65*	*70*	..	110	*90*	125	*60*	*70*	60	..
	W-18			3	*30*	*160*	*125*	205	..	*39*	125	*50*	*30*	60	150	..
	W-7			4	*180*	110	90	*65*	50	*36*	..	*8*	*40*	*90*	*150*	*150*
	W-6			5	..	150	*155*	65	*20*	50	13	..	120	150	45	..
	E-6	110	60	6	..	*100*	*200*	30	*200*	30	85	10	*100*	34	*36*	..
	E-7			7	*45*	..	210	*50*	150	*70*	50	*35*	90	*100*	*20*	..
	E-18			8	110	..	35	*85*	200	80	*150*	50	*55*	100	63	*125*
	E-19			9	*25*	*110*	50	60	125	*130*	175	*125*	90	*75*	*40*	35
	E-30			10	*175*	..	*75*	*25*	*80*	54	40	*40*	30	..	*10*	*24*
1963	W-60	*7*	4	1a	..	*27*	*75*	..	..	65	50	60	*20*	45	50	*8*
	W-59			2a	..	*50*	175	*35*	..	100	75	10	10	35	15	15
	W-56			3a	..	*10*	*10*	10	..	*300*	*30*	60	*175*	*75*	*15*	10
	W-55			5	..	*6*	*75*	*75*	35	8	175	25	60	22	25	*30*

TABLE 2—Continued

Catch in pounds[1] per hour of demersal fishes (species combined) by year, station, depth, transect, and month from Texas and Louisiana, 1962–64
(Night catches are in italics)

Year	Station	Depth M.	Depth Fm.	Transect number	January	February	March	April	May	June	July	August	September	October	November	December
	W-53			5a	..	10	50	20	30	12	140	15	60	30	5	25
	E-52	7	4	6	..	32		*50*	*30*	*115*	130	250	150	*45*	*15*	10
	E-49			7	..	18	*75*	85	175	*80*	*80*	*250*	600	*130*	*150*	70
	E-45			9	..	125	..	265	10	*400*	*280*	20		*110*	100	
	E-44			10	..	40	30	120	*150*	500	30	75	80	*160*	*40*	150
	W-24a	14	7.5	2a	8	*5*	..	*40*	..	85	45	75	75	40	25	40
	W-13a			3a	30	*70*	*15*	35	..	*100*	*320*	150	..	175	*20*	*30*
	W-1			5	*60*	*10*	50	*120*	110	80	120	50	80	*35*	*12*	*45*
	E-1	14	7.5	6	*26*	*50*	*175*	*75*	50	180	140	200	100	240	*300*	*30*
	E-12			7	3	12	46	20	*40*	75	60	*300*	80	200	200	140
	E-24			9	150	*150*	*700*	*8*	55	*80*	*90*	80	*300*	*125*	200	*1,100*
	E-25			10	*135*	300	50	130	*20*	2,000	1,200	125	*450*	*300*	25	100
	W-23a	27	15	2a	*75*	*80*	65	40	100	120	*25*	*60*	460	130	*30*	30
	W-14a			3a	45	65	*120*	50	*25*	*190*	5	*25*	*50*	*110*	*100*	*25*
	W-2			5	*30*	100	*100*	*15*	*40*	*20*	5	*40*	*100*	*100*	*60*	*75*
	E-2	27	15	6	*135*	300	*225*	10	130	*100*	130	*150*	*300*	175	70	60
	E-11			7	140	250	150	*60*	50	15	60	*125*	80	300	..	200
	E-23			9	*1,200*	*1,500*	*2,000*	..	*75*	*750*	*130*	*75*	800	570	200	140
	E-26			10	*180*	200	75	650	35	40	30	10	*400*	*130*	*25*	50
	W-62	46	25	1a	..	*70*	..	..	..	60	10	40	25	*75*	10	*40*
	W-22a			2a	*65*	*15*	30	35	75	60	3	*30*	225	40	..	15
	W-15a			3a	100	200	*35*	*75*	*70*	*190*	25	45	*40*	*150*	*75*	125
	W-3			5	*100*	85	*10*	65	*200*	*150*	*140*	*40*	*30*	*150*	*125*	125
	E-3	46	25	6	*120*	375	*200*	175	70	5	120	*300*	*300*	310	150	80
	E-10			7	120	350	*400*	450	..	*250*	220	*200*	*225*	240	400	75
	E-22			9	150	60	..	100	*150*	*200*	*100*	*30*	*300*	100	130	200
	E-27			10	185	1,000	150	*145*	30	1,000	60	*125*	*200*	250	*75*	200
	W-58	73	40	2a	*150*	70	100	*60*	..	*75*	20	100	200	*50*	*150*	*75*
	W-57			3a	40	35	..	120	*150*	175	15	125	60	*75*	80	*90*
	W-54			5	*70*	*10*	175	35	175	*80*	45	*85*	50	90	*100*	80
	E-51	73	40	6	*125*	225	100	..	40	..	*70*	25	200	*120*	*35*	*28*
	E-50			7	165	*300*	..	*75*	25	*15*	60	150	*150*	15	*150*	*4*
	E-46			9	160	100	100	60	250	*400*	60	*60*	200	80	*125*	*75*
	E-43			10	..	*120*	*350*	*450*	25	100	*70*	*35*	*4*	50	*70*	*320*

TABLE 2—Continued

Catch in pounds[1] per hour of demersal fishes (species combined) by year, station, depth, transect, and month from Texas and Louisiana, 1962–64
(Night catches are in italics)

Year	Station	Depth		Transect number	Month											
		M.	Fm.		January	February	March	April	May	June	July	August	September	October	November	December
	W-6	110	60	5	*30*	*2*	15	*4*	35	40	55	*100*	..	60	110	35
1964	W-60	7	4	1a	8	*25*	*15*	*30*	60	*75*	*50*	10	60	100	35	..
	W-59			2a	*5*	6	8	*53*	*35*	15	70	*40*	100	*150*	*80*	..
	W-56			3a	*75*	12	5	30	367	320	120	80	80	*30*	*10*	..
	W-55			5	*18*	6	15	60	40	40	*200*	*85*	*80*	*20*	*50*	*10*
	W-53			5a	..	..	25	15	18	150	60	*80*	75	65	100	15
	E-52	7	4	6	*5*	*20*	..	60	205	*350*	*150*	*200*	10	*55*	35	*30*
	E-49			7	18	20	.	30	40	300	*120*	30	20	*10*	85	15
	E-45			9	*150*	*1,000*	100	*75*	70	15	75	*35*	*800*	*150*	175	12
	E-44			10	90	*20*	600	60	70	*30*	60	200	300	*10*	300	80
	W-24a	14	7.5	2a	*60*	110	10	*20*	*45*	15	50	*80*	100	*30*	*35*	..
	W-13a			3a	4	15	8	20	400	200	80	160	*75*	*30*	*8*	..
	W-1			5	*8*	*8*	15	*120*	200	45	*250*	*125*	*60*	*15*	*30*	*12*
	E-1	14	7.5	6	*35*	*8*	..	40	50	*6*	*550*	*300*	70	*250*	*53*	*60*
	E-12			7	30	..	60	75	10	200	600	3,600	20	40	*475*	15
	E-24			9	*250*	*150*	93	700	15	..	160	*125*	1,000	*450*	350	15
	E-25			10	.	..		250	60	..	*300*	12	400	5	*80*	*160*
	W-23a	27	15	2a	*30*	*60*	25	30	100	200	15	*15*	65	35	*90*	*30*
	W-14a			3a	35	15	*30*	*35*	120	*40*	10	130	*20*	90	*31*	*26*
	W-2			5	*25*	175	*20*	*100*	*60*	*30*	*25*	*100*	*40*	*60*	*155*	*15*
	E-2	27	15	6	*100*	400	850	*175*	*110*	*80*	*85*	*150*	*250*	*25*	*200*	*15*
	E-11			7	*85*	..	160	*25*	*35*	40	30	50	*300*	500	*208*	600
	E-23			9	1,200	*160*	*460*	500	20	*35*	20	40	225	*200*	230	*600*
	E-26			10	50	*450*	350	175	300	*5*	*220*	30	300	85	*600*	*45*
	W-62	46	25	1a	..	..	..	*75*	45	25	*30*	40	25	*50*	*60*	24
	W-22a			2a	..	..	..	50	*50*	45	40	*60*	90	40	*95*	24
	W-15a			3a	..	..	..	*10*	35	100	*30*	8	..	*75*	*85*	*25*
	W-3			5	*125*	*125*	*170*	*130*	*35*	*200*	50	110	*135*	125	*350*	*30*
	E-3	46	25	6	..	*600*	..	400	125	40	..	300	*150*	75	225	*100*
	E-10			7	.	..	200	*250*	*200*	*300*	*300*	*125*	*125*	*400*	*525*	
	E-22			9	*50*	*110*	..	80	30	30	20	50	15	*200*	100	*30*
	E-27			10	..	..	..	175	*15*	*45*	*40*	30	*150*	350	*350*	*80*
	W-54	73	40	5	85	..	150	100	65	*20*	30	75	..	2	*85*	*60*
	E-46	73	40	9	*50*	..	..	*80*	40	100	2	..	..	*10*	80	..

to 64 m (35 fath) was significantly greater off Louisiana than off Texas each year (Table 3). Differences between the two regions were greatest in the shallow areas and least in deep water in 1962 and 1963. We did not sample at the deepest stations in 1964.

Differences Between Day and Night Catches

Several recent studies have indicated a day-night variation in the catchability of some species of fishes (Boerema 1964; de Groot 1964; Parrish *et al* 1964; Woodhead 1964; Beamish 1966; Hoese *et al.* 1968). We could not make a direct comparison of catches between day and night because samples were not taken at any one station during the day and night on the same cruise.

TABLE 4

Comparisons of mean annual catch between stations within depth contours by a series of analysis of variance tests, 1962–1964

Year	Depth		Coastal region	Stations at which samples were taken	Test results		
						F values	
	M.	Fm.			d.f.	Treatment (stations)	Block (month)
1962	14	7.5	Texas	5	4, 24	0.15	2.03
			Louisiana	5	4, 32	1.26	1.46
	27	15	Texas	5	4, 32	0.49	2.69[1]
			Louisiana	5	4, 25	2.52	1.62
	46	25	Texas	5	4, 36	3.85[1]	1.54
			Louisiana	5	4, 40	0.11	1.64
	64	35	Texas	5	4, 32	0.77	2.65
			Louisiana	5	4, 24	0.85	1.86
	82	45	Texas	5	4, 24	1.28	2.11
			Louisiana	5	4, 28	2.39	2.64
	110	60	Texas	5	4, 20	1.87	0.41
			Louisiana	5	4, 28	1.70	3.53[1]
1963	7	4	Texas	5	4, 32	0.59	1.56
			Louisiana	4	4, 21	0.76	1.50
	14	7.5	Texas	3	2, 16	3.10	1.99
			Louisiana	4	3, 33	1.80	0.74
	27	15	Texas	3	2, 22	1.23	1.51
			Louisiana	4	3, 27	8.21[2]	1.57
	46	25	Texas	4	3, 15	2.00	0.87
			Louisiana	4	3, 27	1.59	1.08
	73	40	Texas	3	2, 18	1.29	1.40
			Louisiana	4	3, 21	0.20	0.89
1964	7	4	Texas	5	4, 32	1.19	1.13
			Louisiana	4	3, 30	1.52	0.72
	14	7.5	Texas	3	2, 20	0.82	1.94
			Louisiana	4	3, 21	0.78	0.85
	27	15	Texas	3	2, 22	0.44	1.11
			Louisiana	4	3, 30	0.79	1.16
	46	25	Texas	4	3, 21	5.57[2]	2.48
			Louisiana	4	3, 18	4.32[1]	2.55

[1] Significance level = 5 percent.
[2] Significance level = 1 percent.

An indirect method that involved two test procedures was used to evaluate day-night differences. First, we assumed that the distribution of fishes among stations at a given depth off the coast of each state was homogeneous. This assumption of homogeneity was tested by a series of two-way analysis of variance tests (stations within a depth and coastal zone were used as treatments and the months in which samples were collected from all stations were used as blocks). Examination of the first five lines in Table 2 and the first line in Table 4 will clarify the test procedure. The assumption of homogeneity appeared valid because 26 of 30 comparisons between stations within depths yielded no significant differences (Table 4).

The second part of the indirect method involved comparisons of day and night catches made with information from adjacent stations when one sample was collected during the day and the other at night within the same week and depth (Table 5). Catches from adjacent stations in transects 5 and 6 (See Fig. 1) were not compared because of the distance between these two transects and because of the differences in catches off Texas and Louisiana. The procedure for selecting pairs of day-night samples for comparison, and the determination of their means are illustrated in Table 6. A paired t-test was used for the comparisons. Only one of the 15 sets of comparisons revealed a significant difference (Table 5). We concluded that differences between day and night catches were negligible.

A study of diel variation in catches (species combined) from 27 m (15 fath) depth and less, off Port Aransas, Texas, yielded significantly larger catches at night (Hoese *et al.* 1968). Diel patterns in catchability varied, however, among species, and also within some of the species. Though most species averaged higher catches at night, some (*Synodus foetens*, *Trichiurus lepturus*, *Poronotus burti*,

TABLE 5

Comparison of relative mean catch between day and night tows off the Louisiana and Texas coast, 1962–1964

Year	Depth		Average catch (pounds/hour)		Test results	
	M.	Fm.	Day	Night	d.f.	t
1962	14	7.5	183	230	50	—0.74
	27	15	214	182	60	0.81
	46	25	149	198	43	—1.66
	64	35	169	142	36	0.77
	82	45	115	127	52	—0.67
	110	60	86	86	49	0.00
1963	7	4	86	107	27	—0.93
	14	7.5	170	188	35	—0.22
	27	15	143	381	27	—2.01
	46	25	124	89	18	0.75
	73	40	111	147	24	—1.39
1964	7	4	72	134	39	—1.77
	14	7.5	399	176	24	1.15
	27	15	209	143	29	1.25
	46	25	81	155	33	—3.04[1]

[1] Significance level = 1 percent.

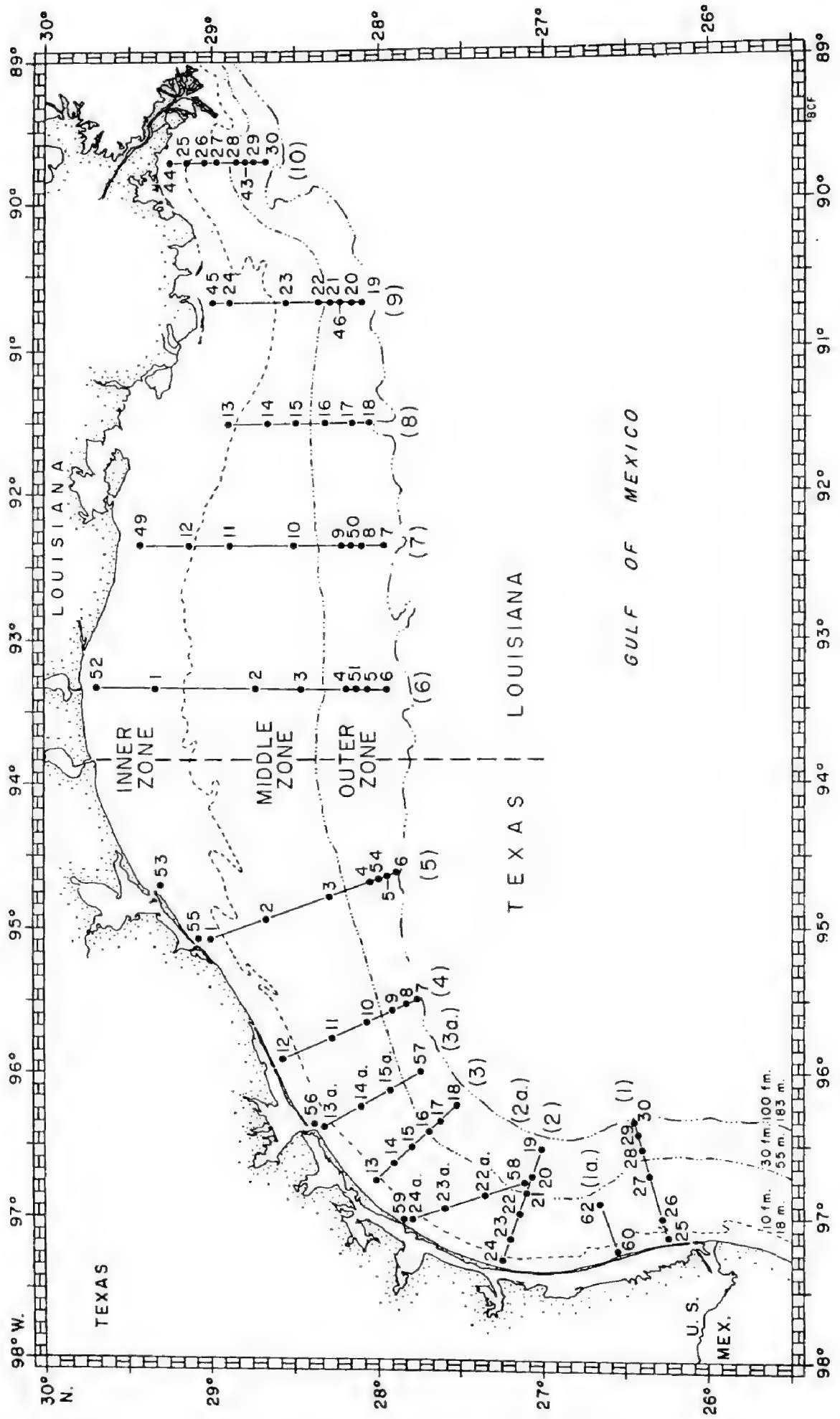

FIG. 1. Locations of stations at which samples were taken during at least 1 year, 1962–1964 (transect numbers in parentheses).

TABLE 6

Example of the pairing procedure for determining day-night differences in catchability
(Data from first 10 lines of Table 2)

Station pairs	Catch (pounds/hour)		Station pairs	Catch (pounds/hour)	
	Day	Night		Day	Night
W 25 and W 24	15	15	E 1 and E 12	45	200
	120	210		35	4
	6	50		60	250
	20	4		60	1,000
	25	25		..	..
	30	5	E 12 and E 13	40	50
	150	210		100	85
	35	200		160	150
	..	..		40	50
W 24 and W 13	25	20		450	200
	40	15		30	4
	10	10		2,500	250
	120	20		..	..
	35	30	E 13 and E 24	300	50
	3	50		225	85
	20	200		40	1,600
	30	90		300	1,250
	35	200	E 24 and E 25	300	450
W 13 and W 12	14	20		300	300
	30	10		1,200	1,600
	65	20		8	200
	35	15		20	300
	125	300		1,500	1,250
	75	40		95	125
	40	90		..	..
	100	65	Total	9,356	11,717
W 12 and W 1	80	15	Mean	183	230
	125	60		..	..
	40	225		..	..
	100	50		..	..

etc.) averaged higher catches during the day. Among the species averaging greater catches at night, one (*Galeichthys felis*) had similar day/night catches in some seasons, while two (*Micropogon undulatus* and *Leiostomus xanthurus*), that were major species in our study, were caught more during the day when the water was turbid. Some or all of the above factor's probably contributed to our finding of diel variation in capture of species combined to be nonsignificant.

Differences Between Years

Annual mean catch by station and year for the stations from which data were collected during at least 6 of the same months in all 3 years is shown in Table 7. Data were compared by a series of two-way analysis of variance tests with years used as treatments and months as blocks. Although catches at most stations varied

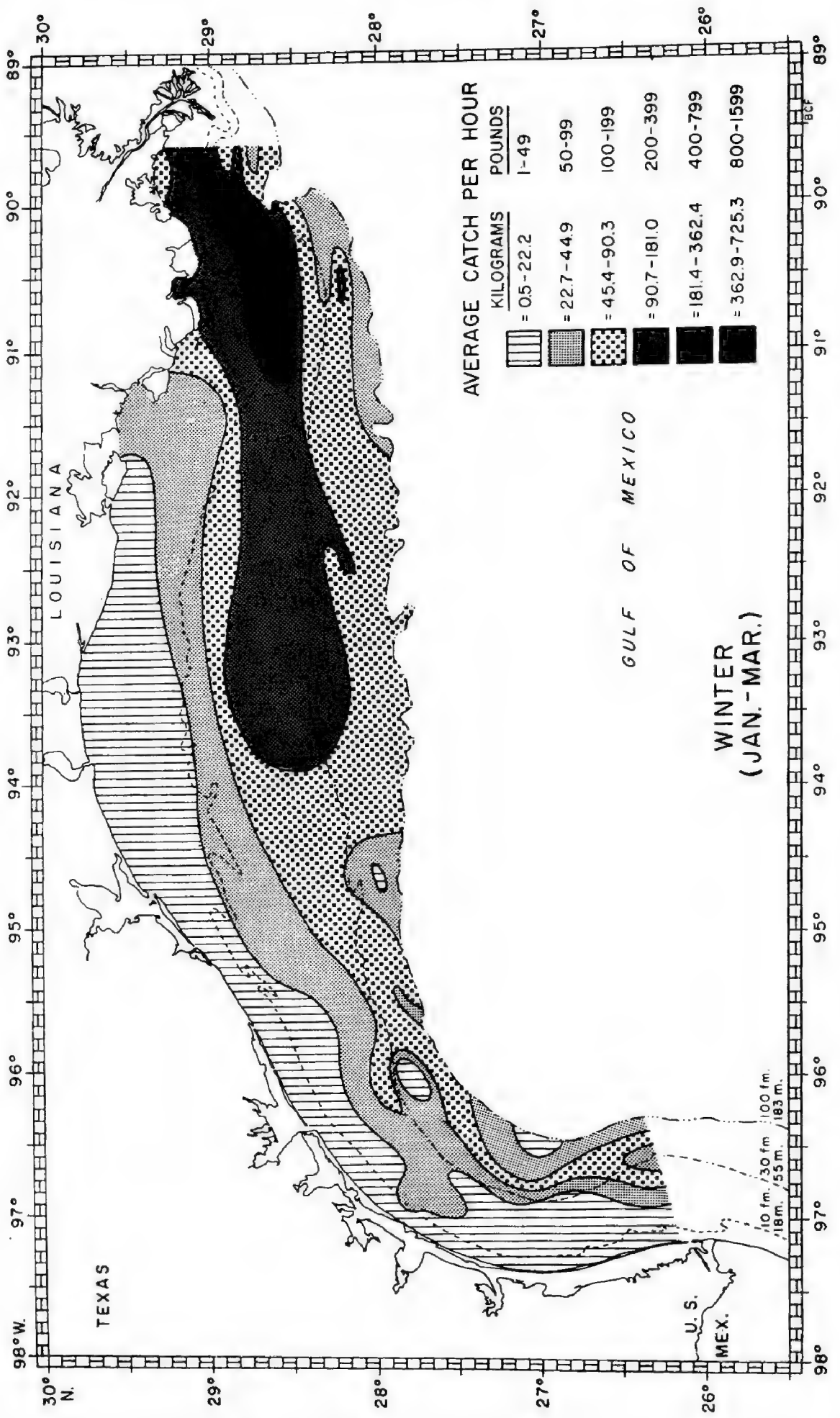

FIG. 2. Relative abundance (by weight) of demersal fishes in the winter (January-March), estimated from the average catch of all fish at each station, 1962–1964.

TABLE 7

Comparisons of average catch between years by station, 1962–1964

Depth		Coastal region	Station number	Number of the same months in which samples were taken each year	Average catch (pounds/hour)			Test results		
									F value	
M.	Fm.				1962	1963	1964	d.f.	Years	Months
14	7.5	Texas	W 1	12	78	64	74	2, 22	0.18	1.99
		Louisiana	E 1	8	221	103	132	2, 14	0.59	0.94
			E 12	8	104	78	574	2, 14	1.29	1.21
			E 24	11	638	269	301	2, 20	3.14	1.96
			E 25	6	575	325	184	2, 10	1.50	1.89
27	15	Texas	W 2	11	66	62	71	2, 20	0.06	0.91
		Louisiana	E 2	12	216	149	203	2, 22	0.74	1.57
			E 11	9	232	109	136	2, 16	2.38	4.51[1]
			E 23	9	444	755	328	2, 16	2.27	1.87
			E 26	11	423	154	230	2, 20	2.62	1.15
46	25	Texas	W 3	11	168	98	140	2, 20	2.22	0.74
		Louisiana	E 3	9	254	196	224	2, 16	0.33	1.65
			E 10	8	269	298	278	2, 14	0.06	0.74
			E 22	11	157	138	65	2, 20	1.50	0.83
			E 27	8	136	229	111	2, 14	0.64	0.63

[1] Significance level = 5 percent.

considerably between years (at most stations catches were greatest in 1962 and lowest in 1963), the differences in abundance between years were not significant at any of the stations (Table 7).

Areal Distribution of Fishes by Season

To illustrate the seasonal distribution of fishes in relation to depth zone, we drew isopleths based on the average catch at each station during a season over the three-year period (Figs. 2, 3, 4 and 5). The seasons were winter (Jan.–Mar.), spring (April–June), summer (July–Sept.), and fall (Oct.–Dec.). In each season, greatest concentrations of fish were centered off central Louisiana and appeared to spread eastward toward the Mississippi River Delta and westward into Texas waters.

Louisiana Coast—In the winter, abundance in the inner depth zone was much greater off the central coast than off the western coast of Louisiana (Fig. 2). The catches in the middle zone were large with the greatest at any depth being made off the central Louisiana coast. In the outer zone, the catches were smaller than in the middle zone.

The concentrations of fishes on the inner and middle zones in the winter apparently spread westward in the spring. Catches in the inner zone in the spring were generally less than in the winter off central Louisiana but greater than in the winter off western Louisiana (Fig. 3). In the middle zone, the fish were much less abundant in the srping, while in the outer zone, concentrations were similar to those in the winter.

Abundance in the summer along the inner zone increased greatly from the

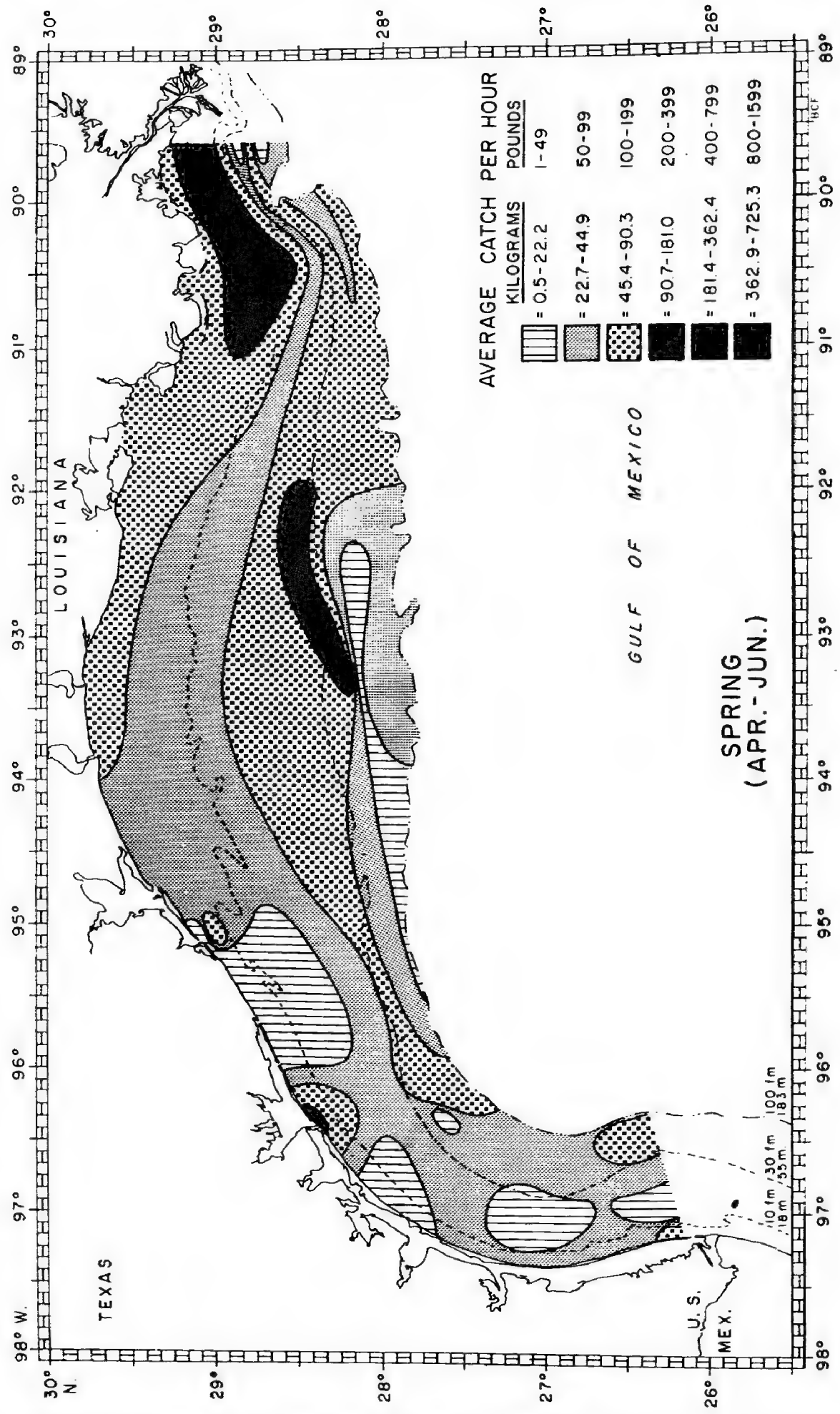

FIG. 3. **Relative abundance (by weight) of demersal fishes in the spring (April-June), estimated from the average catch of all fish at each station, 1962–1964.**

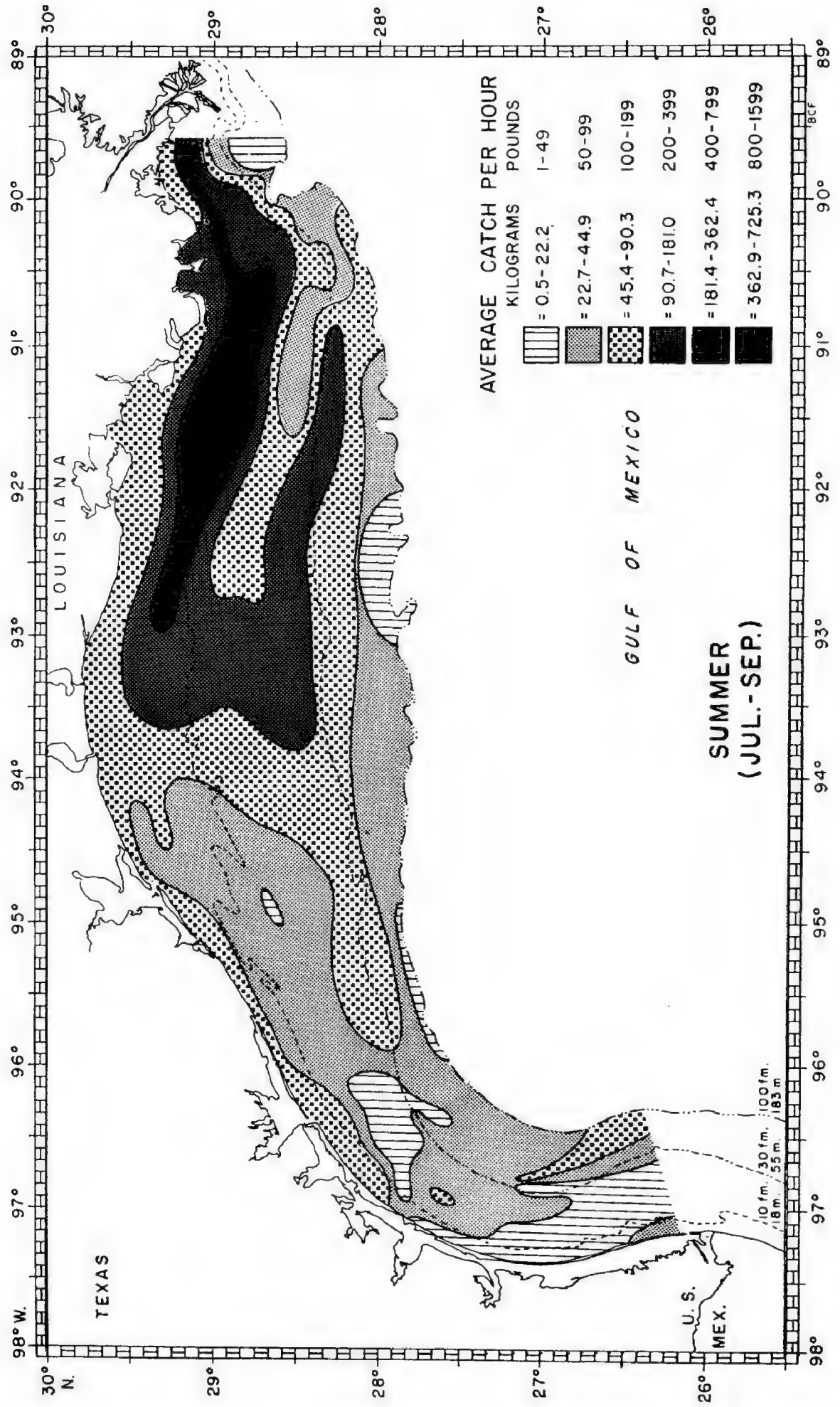

FIG. 4. Relative abundance (by weight) of demersal fishes in the summer (July-September), estimated from the average catch of all fish at each station, 1962–1964.

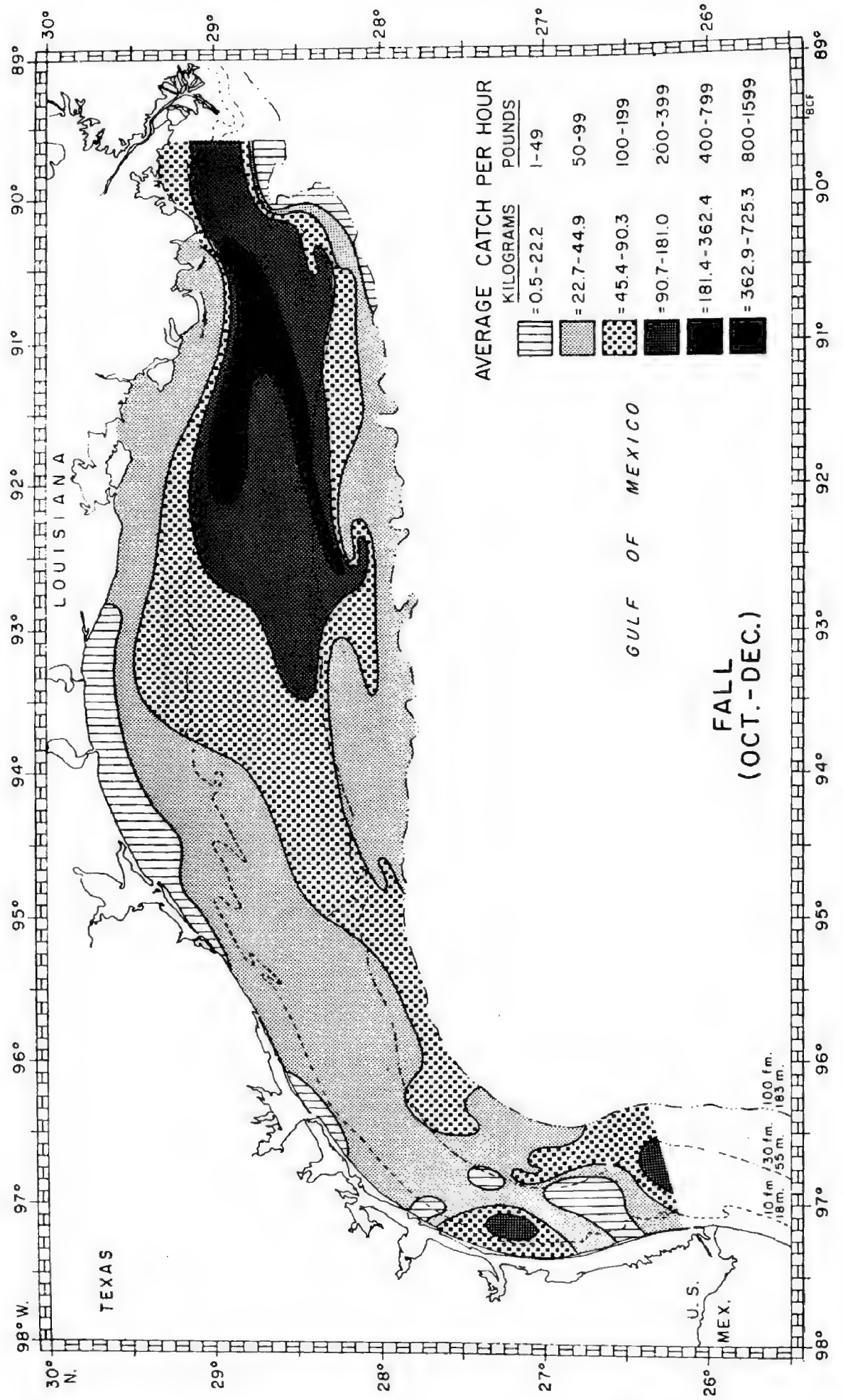

FIG. 5. Relative abundance (by weight) of demersal fishes in the fall (October-December), estimated from the average catch of all fish at each station, 1962–1964.

spring, probably because of recruitment from the estuarine areas (Fig. 4). In the middle zone, there was a moderate increase, in comparison to the winter, off western Louisiana. Abundance in the outer zone in the summer was similar to that in the spring.

In the fall, concentrations in most of the inner zone, especially off western Louisiana, decreased from the summer (Fig. 5). The catches on most of the middle and outer zones were about the same as in the summer but were not as large as in the winter (Fig. 2).

Texas Coast—In the winter, catches in the inner zone were very low (Fig. 2). The fish became more abundant in the deeper parts of the middle zone. The highest concentrations occurred in most of the outer zone.

Abundance in the parts of the inner zone near tidal passes, especially at Pass Cavallo, Stations (W) 56 and 13a, was greater in the spring than in the winter (Fig. 2, 3). The concentrations in the middle zone were similar to the winter, while in most areas of the outer zone they were less than in the winter.

In the summer, the catches in the inner zone off eastern Texas increased from the spring in areas located away from the tidal passes, whereas they decreased off southern Texas (Fig. 4). Abundance in the middle and outer zones changed little.

The concentrations in the fall in the inner zone decreased from the summer off eastern Texas and increased off parts of southern Texas (Fig. 5). In the middle and outer zones, the catches increased off southern Texas near Mexico, and changed little on the rest of the coast from the summer. The greatest change from the fall to the winter was the decrease in abundance along the inner zone (Fig. 2).

SPECIES COMPOSITION

Species of demersal fishes that constituted an estimated one percent or more of the total catch by weight (data from all years and areas combined) are listed in Table 8. The Atlantic croaker, *Micopogon undulatus*, an estuarine species, and the longspine porgy, *Stenotomus caprinus*, an offshore species, dominated the catches. Based on those species which constituted five percent or more of the average total catch in various seasons and depth zones, differences in species composition did exist between catches made off Louisiana and those off Texas (Tables 9 and 10).

The Atlantic croaker, longspine porgy, sand seatrout, *Cynoscion arenarius*, and sea catfish, *Galeichthys felis*, were most abundant in catches off Louisiana when depth zones and seasons were combined (Table 9). The relative abundance of some of the demersal species in each depth zone did vary, however, between seasons. In the inner zone, the catches of croaker and sea catfish ranked first and second in all seasons. In the middle zone, the croaker ranked first and the longspine porgy second during the winter and fall; the rank of these two species was reversed in the spring and summer. Croaker and longspine porgy ranked first and second, respectively, in abundance in all seasons in the outer zone.

Off Texas, longspine porgy, Atlantic croaker, inshore lizardfish, *Synodus foetens*, and silver seatrout, *Cynoscion nothus*, led in abundance when depth zones

TABLE 8

Species that constituted one percent or more of the average catch by weight of all demersal fishes caught off Louisiana and Texas, 1962–64

Species	Percent of total catch		
	Louisiana	Texas	Entire coast
Atlantic crocker, *Micropogon undulatus*	35	9	28
Longspine porgy, *Stenotomus caprinus*	18	21	19
Inshore lizardfish, *Synodus foetens*	3	9	5
Sand seatrout, *Cynoscion arenarius*	5	5	5
Sea catfish, *Galeichthys felis*	5	2	4
Silver seatrout, *Cynoscion nothus*	3	7	4
Blackfin searobin, *Prionotus rubio*	4	2	4
Spot, *Leiostomus xanthurus*	4	4	4
Rock sea bass, *Centropristis philadelphicus*	2	4	3
Atlantic cutlassfish, *Trichiurus lepturus*	2	2	2
Southern kingfish, *Menticirrhus americanus*	1	3	2
Gulf butterfish, *Poronotus burti*	1	4	2
Wenchman, *Pristipomoides aquilonaris*	1	5	2
Shoal flounder, *Syacium gunteri*	1	4	2
Mexican searobin, *Prionotus paralatus*	1	4	2
Mexican flounder, *Cyclopsetta chittendeni*	1	2	1
Star drum, *Stellifer lanceolatus*	1	1	1
Red goatfish, *Mullus auratus*	.	2	1
Bumper, *Chloroscombrus chrysurus*	1	1	1

and seasons were combined (Table 10). The most abundant species in the inner zone in each season was: southern kingfish, *Menticirrhus americanus*, in the winter and fall; silver seatrout in the spring; and Atlantic croaker in the summer. The second most abundant species in the winter, spring, summer and fall were spot, Atlantic croaker, sand seatrout, and Atlantic croaker, respectively. Longspine porgy ranked first in abundance in the middle zone in all seasons except spring when the inshore lizardfish dominated catches. Species ranking second in abundance were sand seatrout in the winter, longspine porgy in the spring, and Atlantic croaker in the summer and fall. In the outer zone, longspine porgy were the most abundant in all seasons and the inshore lizardfish was the second most abundant species in all seasons except winter when the wenchman, *Pristipomoides aquilonaris*, ranked second.

DISCUSSION

Large catches in the middle zone off Louisiana in the winter (Fig. 2) apparently were a result of Atlantic croakers moving offshore into water where longspine porgies were abundant (Table 9). Gunter (1938, 1945) noted that croakers were scarce in estuaries and along the adjacent coastlines in the fall and winter. The catches off Louisiana in which croaker predominated were made more shoreward in the spring than in the winter, and were generally separated from the catches offshore in which longspine porgy were most abundant (Fig. 3 and Table 9). Large catches, in which croaker predominated, also were made on the inner

TABLE 9

Species that constituted five percent or more of the average catch by weight of all demersal fishes caught off Louisiana, 1962–1964
(Listed by season and depth zone)

	Season									
	Winter (Jan.–March)		Spring (April–June)		Summer (July–Sept.)		Fall (Oct.–Dec.)		All seasons (Jan.–Dec.)	
Depth zone	Species	Percent of total catch	Species	Percent of total catch	Species	Percent of total catch	Species	Percent of total catch	Species	Percent of total catch
Inner zone	Atlantic croaker	51	Atlantic croaker	49	Atlantic croaker	48	Atlantic croaker	66	Atlantic croaker	52
7–14 m.	Sea catfish	10	Sea catfish	14	Sea catfish	8	Sea catfish	8	Sea catfish	10
(4–7.5 fm.)	Southern kingfish	7	Sand seatrout	6	Sand seatrout	8			Sand seatrout	6
	Longspine porgy	5	Atlantic cutlassfish	5	Spot	7			Spot	5
			Spot	5	Atlantic cutlassfish	6				
Middle zone	Atlantic croaker	39	Longspine porgy	27	Longspine porgy	29	Atlantic croaker	40	Atlantic croaker	31
27–46 m.	Longspine porgy	22	Atlantic croaker	20	Atlantic croaker	21	Longspine porgy	20	Longspine porgy	24
(15–25 fm.)			Inshore lizardfish	10	Blackfin searobin	5	Silver seatrout	6	Silver seatrout	6
			Atlantic cutlassfish	7			Blackfin searobin	5	Blackfin searobin	5
			Blackfin searobin	7			Spot	5		
			Sand seatrout	6						
Outer zone	Longspine porgy	31	Longspine porgy	38	Longspine porgy	54	Longspine porgy	23	Longspine porgy	35
64–110 m.	Inshore lizardfish	10	Blackfin searobin	11	Mexican flounder	6	Atlantic croaker	12	Blackfin searobin	9
(35–60 fm.)	Atlantic croaker	9	Atlantic croaker	9	Rock sea bass	6	Blackfin searobin	9	Atlantic croaker	8
	Blackfin searobin	8	Rock sea bass	9	Blackfin searobin	5	Sand seatrout	9	Rock sea bass	7
	Rock sea bass	5					Rock sea bass	7	Inshore lizardfish	6
							Spot	7		
Entire shelf	Atlantic croaker	36	Atlantic croaker	28	Atlantic croaker	33	Atlantic croaker	41	Atlantic croaker	35
7–100 m.	Longspine porgy	20	Longspine porgy	19	Longspine porgy	17	Longspine porgy	16	Longspine porgy	18
(4–60 fm.)			Sea catfish	6	Sand seatrout	6	Blackfin searobin	6	Sand seatrout	5
			Sand seatrout	5	Sea catfish	6	Sand seatrout	5	Sea catfish	5
			Inshore lizardfish	5	Spot	5				
			Blackfin searobin	5						
			Atlantic cutlassfish	5						

TABLE 10

Species that constituted five percent or more of the average catch by weight of all demersal fishes caught off Texas, 1962–1964

(Listed by season and depth zone)

	Season									
	Winter (Jan.–March)		Spring (April–June)		Summer (July–Sept.)		Fall (Oct.–Dec.)		All seasons (Jan.–Dec.)	
Depth zone	Species	Percent of total catch	Species	Percent of total catch	Species	Percent of total catch	Species	Percent of total catch	Species	Percent of total catch
Inner zone	Southern kingfish	26	Silver seatrout	26	Atlantic croaker	30	Southern kingfish	23	Atlantic croaker	20
7–14 m.	Spot	19	Atlantic croaker	15	Sand seatrout	9	Atlantic croaker	10	Silver seatrout	14
(4–7.5 fm.)	Sand seatrout	12	Sea catfish	10	Silver seatrout	7	Sand seatrout	9	Southern kingfish	11
	Silver seatrout	7	Spot	7	Seat catfish	6	Silver seatrout	7	Sea catfish	7
			Southern kingfish	5	Southern kingfish	5	Sea catfish	5	Spot	7
			Atlantic cutlassfish	5			Shoal flounder	5	Sand seatrout	5
							Longspine porgy	5		
Middle zone	Longspine porgy	38	Inshore lizardfish	15	Longspine porgy	25	Longspine porgy	26	Longspine porgy	27
27–46 m.	Sand seatrout	8	Longspine porgy	15	Atlantic croaker	9	Atlantic croaker	12	Inshore lizardfish	9
(15–25 fm.)	Inshore lizardfish	7	Shoal flounder	14	Inshore lizardfish	9	Shoal flounder	8	Shoal flounder	9
	Shoal flounder	7	Gulf butterfish	11	Silver seatrout	9	Spot	8	Atlantic croaker	7
	Rock sea bass	6	Rock sea bass	9	Sand seatrout	7	Inshore lizardfish	7	Sand seatrout	7
	Atlantic croaker	5	Silver seatrout	6	Shoal flounder	5	Silver seatrout	6	Silver seatrout	5
									Rock sea bass	5
Outer zone	Longspine porgy	29	Longspine porgy	26	Longspine porgy	26	Longspine porgy	27	Longspine porgy	27
64–110 m.	Wenchman	18	Inshore lizardfish	16	Inshore lizardfish	14	Inshore lizardfish	13	Inshore lizardfish	14
(35–60 fm.)	Inshore lizardfish	12	Wenchman	12	Wenchman	12	Wenchman	12	Wenchman	14
	Mexican searobin	9	Rock sea bass	6	Mexican searobin	8	Mexican searobin	8	Mexican searobin	8
			Mexican searobin	6	Rock sea bass	6	Rock sea bass	5	Rock sea bass	5
Entire shelf	Longspine porgy	28	Silver seatrout	12	Atlantic croaker	17	Longspine porgy	24	Longspine porgy	21
7–110 m.	Inshore lizardfish	9	Longspine porgy	11	Longspine porgy	15	Atlantic croaker	8	Atlantic croaker	9
(4–60 fm.)	Wenchman	8	Inshore lizardfish	9	Inshore lizardfish	7	Inshore lizardfish	8	Inshore lizardfish	9
	Sand seatrout	6	Gulf butterfish	7	Silver seatrout	6	Sand seatrout	6	Silver seatrout	7
	Mexican searobin	5	Atlantic croaker	6			Shoal flounder	5	Wenchman	5
			Shoal flounder	5					Sand seatrout	5
			Rock sea bass.	5						

shelf westward to Texas. Hildebrand (1954) reported that croakers were abundant in trawl catches off the Louisiana-Texas border in June. We made large catches in the inner depth zone along eastern Texas in the summer (Fig. 4), the only season that croakers were most abundant on the inner zone off Texas (Table 10). In the fall, a return toward the winter densities—low in the inner zone off eastern Texas and western Louisiana, and high in the middle zone off Louisiana (Fig. 5)—probably reflected the movement of croakers offshore again (Tables 9 and 10).

In our catches, the species that are definitely associated with the estuaries (*Micropogon undulatus*, *Cynoscion arenarius*, *Galeichthys felis*, *Leiostomus xanthurus*, and *Menticirrhus americanus*) usually had great seasonal variation, probably because they spend part of their life cycle inshore of the area studied. The seasonal variations in catches of species that are never associated with the estuaries (*Stenotomus caprinus*, *Prionotus rubio*, *Centropristis philadelphicus*, *Pristipomoides aquilonaris*, *Syacium gunteri*, *Prionotus paralatus*, *Cyclopsetta chittendeni*, and *Mullus auratus*) were usually much less than those exhibited by the estuarine species.

The average annual concentrations of fish were high at some of the easternmost stations, and decreased markedly to the west (Fig. 6). This area off Louisiana is in the western half of a region that Gunter (1967) has called one of the world's most productive fishery areas.

Most of this area lies within the shelf that van Andel and Curray (1960) reported as having active deposition of silts and clays together with some suspended material brought directly from the Mississippi River by currents. They also indicated that most of the shelf off western Louisiana and eastern Texas is nondepositional and, therefore, has much more sand, while most of the southern Texas shelf has moderate depositional activity due to a north-south convergence of currents carrying sediments from three rivers along the Texas coast. Our study indicated that the area off southern Texas (Fig. 6) may include the northern tip of an offshore concentration of demersal fishes off northern Mexico.

Average catches made in this study are lower than that which a commercial fleet would realize for at least two reasons. First, the fleet fishes with more efficient gear, such as the balloon type trawls described by Bullis *et al* (1960), and, second, fishing practices are more efficient, i.e., fish concentrations are sought out, and, when found, fished repeatedly. To provide fishermen with an indication of how much greater their catches might be, without attempting to adjust for all the variables involved, we have used two reports—one on the commercial catch and the other on some exploratory trawling off part of the Louisiana coast—to make some general comparisons with our data.

Roithmayr (1965) reported the average catch by the industrial demersal fishery during 1959–63 to be 408 kg (900 lb.) per hour, in 13–55 m (7–30 fath) off central Louisiana (89°–91° 25′ W long). In the same area between 14 and 46 m (7.5 and 25 fath) on transects 9–10 during 1962–64, we made an average catch of 138 kg (305 pounds) per hour. The commercial catch in this instance was about three times greater than our catches. Soviet-Cuban investigators (Sal'nikov) 1966) made catches of 200–750 kg (440–1,650 lb.) per hour in 40–80 m (22–44

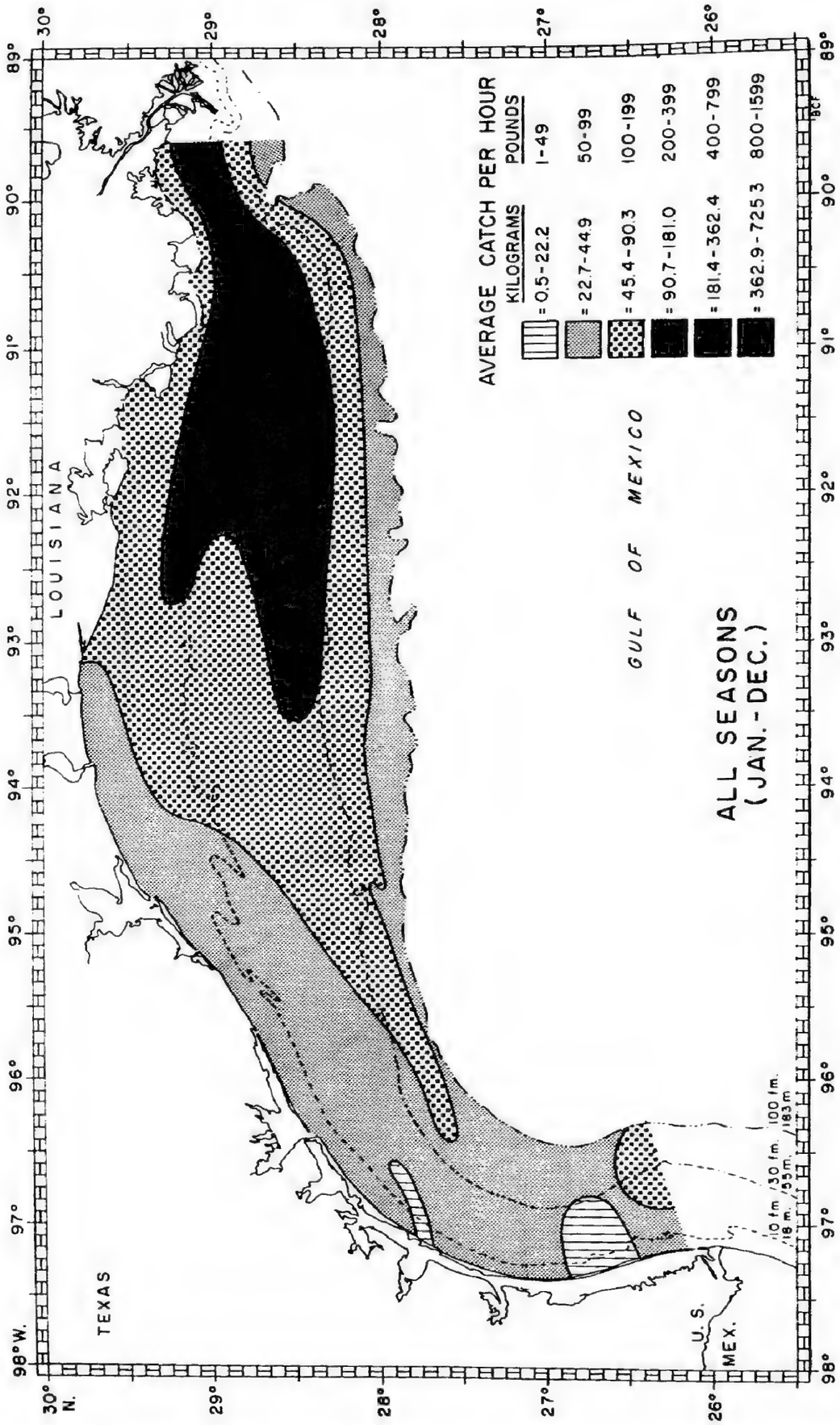

FIG. 6. Relative abundance (by weight) of demersal fishes from 1962–1964, estimated from the average catch of all fish at each station.

fath) off Louisiana (91°–93° W long) during March 1963 with fish trawls. In contrast, our catches averaged less than 159 kg (350 lb.) per hour at each station in the same area during the winter in 1962–64.

Our study indicated that the greatest catches of demersal fishes could have been made in 13–37 m (7–20 fath) off Louisiana between 90°–91° W long during the winter and in 9 to 18 m (5–10 fath) during the summer. Greatest catches in the fall could have been made in 9–37 m (5–20 fath) off Louisiana between 90.5°–92° W long, whereas the best catches in the spring could have been made in 9–18 (5–10 fath) off the Louisiana coast between 89.5°–90° W long. Atlantic croaker would probably have dominated the catches at all the above locations. Any fishery that attempts to catch predominantly longspine porgy would make the best catches during any season in 37–55 m (20–30 fath) off western Louisiana between 92°–93° W long.

SUMMARY

The average catch of bottomfish was about three times greater off Louisiana (93 kg/hr; 204 lb/hr) than off Texas (35 kg/hr; 77 lb/hr). Differences in mean catch between Texas and Louisiana were greatest in the shallow areas and generally became less in deeper water. Catches of bottomfish (species combined) in day and night tows were similar. Differences in abundance between years at a particular station were sometimes great, but not statistically significant. At most stations catches were greatest in 1962 and lowest in 1963. Seasonal differences in abundance were great off Texas and Louisiana. Off Louisiana, the most dense concentrations of fishes were in the winter and summer. Off Texas, the highest concentrations were in the summer and fall. The greatest concentrations of fish were in the inner (2–18 m; 1–10 fath) and middle 20–55 m; 11–30 fath) depth zones off Louisiana, whereas the greatest concentrations occurred in the middle and outer zones off Texas. Atlantic croaker and longspine porgy constituted nearly half of the total catch. Atlantic croaker, longspine porgy, sand seatrout and sea catfish were caught in greatest abundance off Louisiana. Longspine porgy, Atlantic croaker, inshore lizardfish and silver seatrout were predominant in the catches off Texas.

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We gratefully acknowledge the assistance given by various staff members in completing this study. We especially wish to note the assistance given by Robert F. Temple and Richard A. Neal in their suggestions and in critically reviewing the manuscript and by John B. Hervey in processing the data.

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THE REPRODUCTIVE BIOLOGY AND LARVAL DEVELOPMENT OF *LAEONEREIS CULVERI* WEBSTER (POLYCHAETA; NEREIDAE)

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ABSTRACT

Laeonereis culveri is a tubiculus, dioecious estuarine polychaete that resides in an environment characterized by large fluxuations of salinity and temperature. Its reproductive habits follow those characteristic of fresh to brackish water nereids. Oogenesis is initiated in the lateral peritoneum, giving rise to demersal pale yellow ova 200 μm in diameter. Spermatogenesis begins in a similar location giving rise to "sperm plaques" which disrupt into individual spermatozoa upon reaching maturity. Early development and larval development are typical of the Nereidae in general.

INTRODUCTION

Representatives of the Family Nereidae have a world wide distribution and number close to three hundred fifty species (Hartman 1959). The nereids, being fairly common, large and having such striking features in the life history of some species as swarming and the heteronereid transformation have long attracted the attention of investigators in various disciplines. It is somewhat surprising therefore, that the development of relatively few species has been worked out. Only nine nereid species have been reared to sexual maturity and twelve other nereid species have been studied specifically with regard to reproduction and development (Reish 1957). This study presents an account of gametogenesis and the early larval development of *L. culveri*. This polychaete has, heretofore, remained uninvestigated with the exception of the osmoregulatory examination of Oglesby (1965a & b) and the ecological survey of Hedgpeth (1950). *L. culveri* makes a significant contribution to the food chains of the salt flats in the numerous bay systems along the Texas Gulf coast (Hedgpeth, 1950) thus it is hoped that a knowledge of the reproductive biology of this important nereid will aid our understanding of these productive estuarine areas.

MATERIALS AND METHODS

Specimens of *L. culveri* were collected weekly from a single population located on the southwest portion of Harbor Island, Redfish Bay, Texas (Fig. 1), during the period from August 1969 to March 1970 and observations on environmental conditions were made at that location (Table 1).

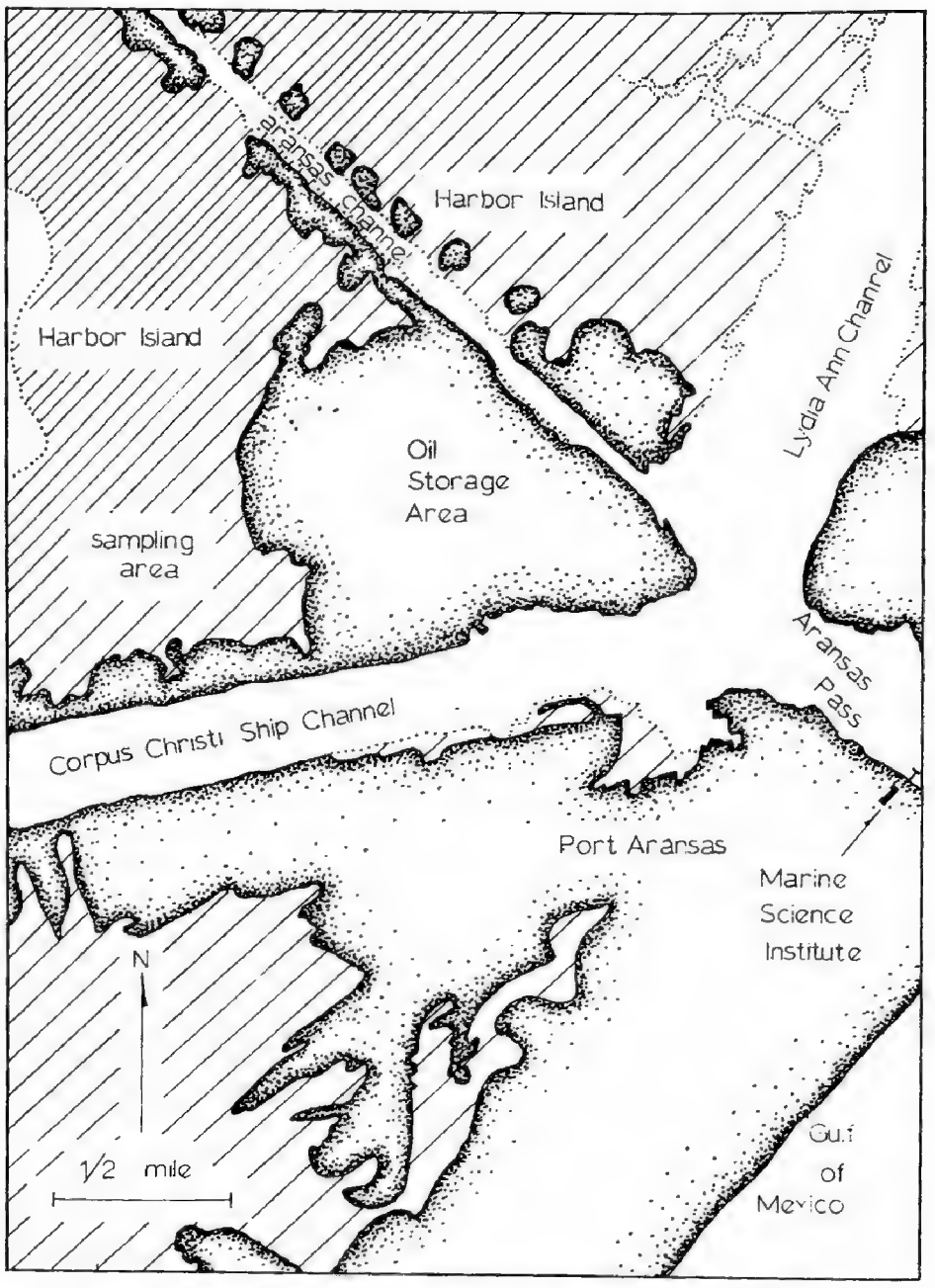


FIG. 1. Study area and the general area of investigation, with the approximate limits of occasional inundation shown by the cross hatching, stippled areas indicate approximate limits of low water.

Environmental parameters for the suspected and definite spawning periods:

Water °C	Substrate °C	Salinity
26.3	24.0	43.5‰

Environmental parameters for the definite spawning periods:

Water °C	Substrate °C	Salinity
27.3	24.0	44.0‰

Sexually mature adults were collected by turning over a square meter of substrate to a depth of several centimeters and routinely sorting out the animals present. The method originally described by Newell (1949) was used to sample for the larvae of this polychaete.

Artificial fertilizations were obtained by mixing the gametes shed from mature individuals in Petri dishes containing filtered sea water. Spontaneous shedding of gametes occurred infrequently, thus necessitating the slitting of the animal either at the base of a parapodium or between two adjacent parapodia to obtain gametes. With male specimens the sperm suspension would rapidly stream from the incision, however with the females it was often necessary to slit several consecutive segments to obtain 100 to 200 mature ova. Twenty minutes were allowed for fertilization at 22°C after which the ova were gently swirled to the center of the dish and the sperm suspension carefully pipetted off and fresh sea water added. The fertilized ova were found to develop well in the Petri dishes with only daily changing of the water required for them to reach the setigerous

TABLE 1

Collection date	Temperature (°C) Water	Substrate	Salinity (‰)	Population density (animals/m²)	Weight range (mg)	Ova and sperm plaque size with additional notes on maturity
1969						
13 June	29.4	29.4	38.4	65	.....	♀ <20 μm & 60 μm
29 July*	29.4	29.4	38.4	127	.....	♀ 100 μm; ♂ 15–30 μm
5 Aug.	31.6	29.4	44.0	54	.....	♀ <20 μm to 40 μm; ♂ 15–30 μm
18 Aug.*	31.6	28.8	63.9	68	.....	no measurements; green coloration
25 Aug.**	32.2	30.5	54.0	105	.....	no measurements; advanced histolysis
2 Sept.**	33.9	29.4	43.7	54	.....	♂ spawned; ♀ 150.8 μm
9 Sept.**	30.5	28.8	51.5	54	.....	♂ spawned; ♀ 200 μm
23 Sept.**	28.8	27.2	34.2	35	.....	♂ spawned; ♀ 108 μm
7 Oct.	22.2	23.2	34.5	46	.....	♀ 50 μm
28 Oct.*	18.5	20.0	29.0	108	.....	no measurements; green coloration
9 Dec.	13.0	14.0	28.0	203	.....	no measurements
11 Dec.	11.5	13.0	32.0	70	2.7/43.0	♀ 40 μm; ♂ immature
16 Dec.	29.0	24.0	34.5	97	9.8/47.9	♀ 30–50 μm; ♂ immature
1970						
8 Jan.	5.0	8.0	29.0	41	21.8/66.5	♀ 40–70 μm
13 Jan.	10.0	11.5	24.0	27	4.4/29.0	♀ 20–40 μm
21 Jan.**	15.0	12.0	41.7	108	0.9/122.4	♂ & ♀ spawned in lab
27 Jan.**	23.5	22.0	28.7	108	9.2/74.5	♀ 200 μm
7 Feb.*	19.5	18.0	39.0	165	5.0/79.5	green coloration
18 Feb.**	...	17.0	54.0	105	5.6/83.8	♀ spawned 200 μm; no ♂
Averages	23.03	21.87	39.07	86.3	.....	.....

* Suspected spawning period.
** Definite spawning period.

larval stages. Unfortunately the larvae could not be cultured beyond this point and although they were observed to feed on blue-green algae and diatoms added to their culture dishes, further segment proliferation was not observed. Since these forms are benthic it may be that a proper substrate is required for further growth along with the proper diet.

For photography larvae were narcotized with a 7.5% solution of magnesium chloride hexahydrate (Pantin 1946) and viewed under phase contrast optics.

Paraffin sections of adult specimens were cut at 6, 8, and 10 μm after fixation in alcoholic Bouin's and stained with either Ehrlich's haematoxylin counterstained with eosin (Humason 1967) or Masson's trichrome stain (Gurr 1963). Strong Flemming's solution was used as the fixative to observe the localization of "lipid" materials within the ova and parenchymal tissue (Baker 1957).

REPRODUCTION

Maturational Changes

L. culveri inhabits weakly chitinized burrows in a mud-sand substrate and forms relatively extensive beds with population densities reaching 203 animals/m² (Table 1). The beds of this polychaete are subject to wide temperature and salinity variations, 8.0 to 30.5°C and 2.0 to 64.0‰ (Hedgpeth 1953 and Table 1).

These variations are due principally to the shallow overlying water being acted upon by the constant southeast or occasional harsh north winds and solar radiation.

The tubiculous adult of *L. culveri* is a dioecious atoke that measures 6 to 8 cm and fails to exhibit any sexual dimorphism up until the time of sexual maturity. As sexual maturity is reached there is seen an accompanying color change that alters the characteristic red-orange of the immature adult to the greenish hue of the sexually mature. It is at this stage that the males and females can be clearly differentiated. The male appears light green to yellow owing to the presence of sperm within the coelom, whereas the female appears a much deeper olive green. Similar coloration changes have been seen in several other species of nereids, namely *Nereis diversicolor* (Dales 1950) and *Nereis japonica* (Izuka 1908). In *N. diversicolor* the color change has been attributed to the accumulation of the green pigment biliverdin, resulting from an increased breakdown of haemoglobin concomitant with tissue histolysis (Dales and Kennedy 1954). Extensive tissue histolysis also occurs in *L. culveri*, with a great reduction of the body wall musculature, septa and intestinal tract, thus it is not likely that the accumulation of biliverdin as found in *N. diversicolor* is also responsible for the color change in *L. culveri*.

Gametogenesis

The first evidence of the formation of the reproductive system is presented by the appearance of the primordial germ cells. These cells are separated from the line of body cells at a very early developmental stage, but fail to cleave further for some time thereafter, lying among the mesodermal cells of the splanchnic layer (Okada 1968). About the time the peritoneum reaches its full development the primordial germ cells make their appearance in special regions of the septa, which in *L. culveri* appears to be the peritoneal lining of the parapodia and a U-shaped region adjacent to each septum. The initiation of gametogenesis begins with the primordial germ cells undergoing a rapid proliferation and releasing germ cells into the body cavity where they mature into either ova or spermatozoa, dependent upon the genotypic sex of the animal.

Oogenesis

Oogonia are first evident as small cells, less than 5 μm in diameter, occurring in clusters of from six to eight cells each, often in what appears to be a basophilic matrix. The nuclei of the oogonia are vesicular, containing dense chromatin material in prophase activity appearing as clumps or knots (Fig. 2), whereas the cytoplasm occupies little more than a thin layer around the nucleus. In this stage the developing oogonia are rather difficult to distinguish from spermatogonia in the same relative stage of development, making the sexing of animals in early gametogenesis difficult. The first definite sign of sexual difference between the young gametes is after the oogonal clusters have fragmented and have been released into the coelom. At the time of release into the coelom, the oocyte is from 10 to 15 μm in diameter and its spherical nucleus is characterized by the relaxation of the dense chromatin masses into a reticulum which typlifies the "resting" nucleus (Cohn 1964), a nucleolus begins to appear and the cytoplasmic volume

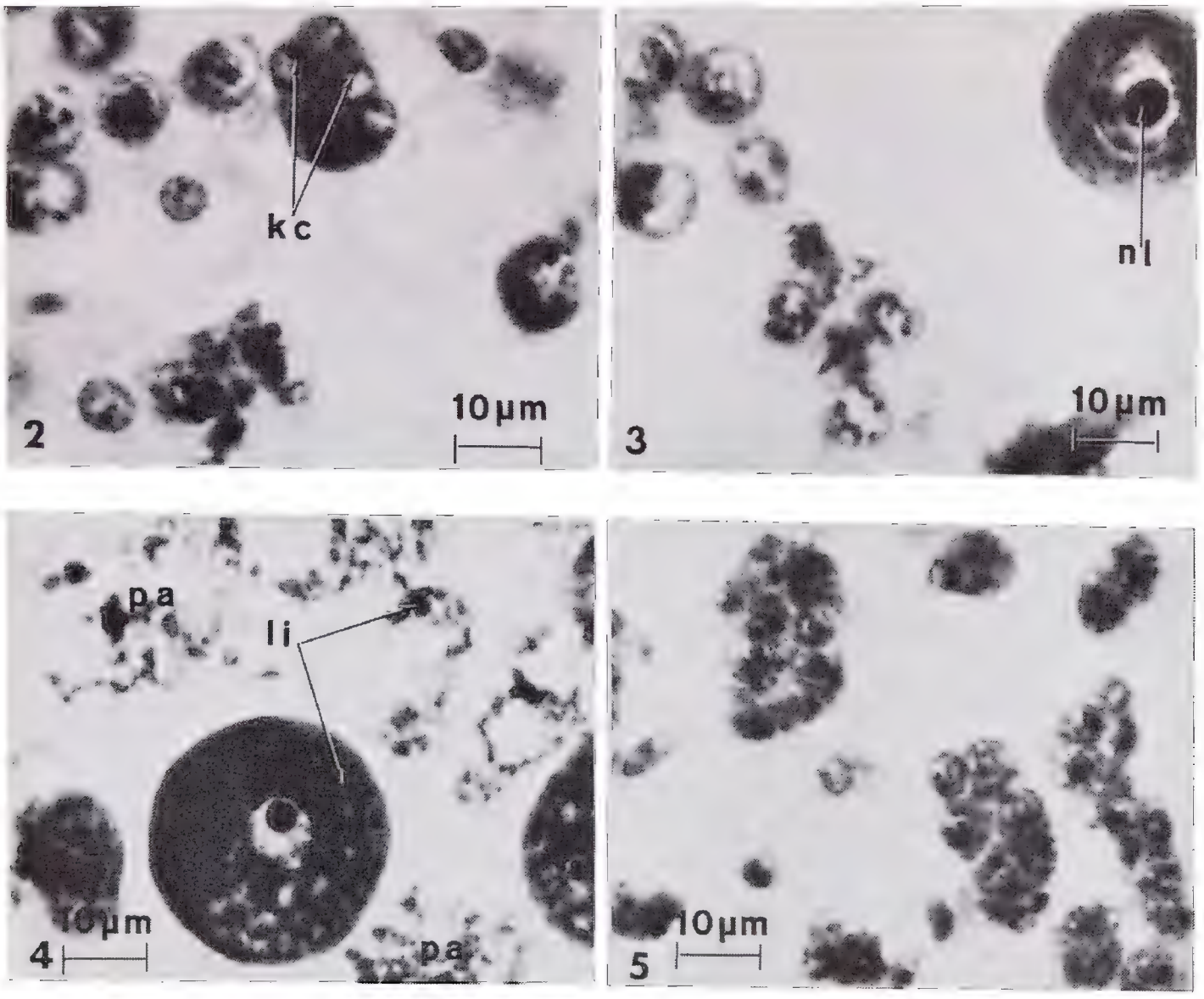


FIG. 2. Clusters of 5 μm oogonia showing knotted chromatin (kc); 1000 X, Masson's Tri-chrome.

FIG. 3. Individual oocytes of approximately 10 μm in diameter are seen in the upper left while a single more mature oocyte, 30 μm in diameter, with its now conspicuous nucleolus (nl) is seen at the upper right of this figure. 1000 X, Masson's Tri-chrome.

FIG. 4. An ovum and extensive parenchymal tissue (pa) showing the blackened lipid inclusions (li) common to both. Fixed in strong Flemming's solution, 1000 X, H and E.

FIG. 5. Young spermatogonia existing in clumps similar to the oogonia (see fig. 2). 1000 X, Masson's Tri-chrome.

FIG. 6. Sperm plaques, 30 μm in diameter, exhibiting chromatin condensation (cc). 400 X, H and E.

FIG. 7. Cross section of a male after complete fragmentation of sperm plaques within the coelomic cavity, note the greatly flattened gut resulting form the amount of sperm present and the rounded heads of the spermatozoa. 400 X, H and E.

begins to increase (Fig. 3). Upon reaching a diameter of 20 to 30 μm the germinal vesicle remains spherical with its contents completely in a uniform network; the nucleolus is now very prominent, being slightly more basophilic than the surrounding nuclear reticulum; and the cytoplasm is beginning to exhibit the initiation of yolk deposition as well as an increased amount of dense basophilic material, the latter due possibly to a movement of nuclear materials into the cytoplasm (Balinsky 1960). From this stage onward no marked nuclear changes occur. At about this time another tissue is beginning to appear within the coelom. The parenchymal tissue (Dales 1950) has its origin from a location similar to that of the germ cells and has been said to contribute to yolk deposition and secondarily to tissue histolysis in other nereids (Dales 1950, McIntosh 1907, Herpin 1925 and Clark 1961). Preliminary observations on the lipid content of the parenchymal tissue have shown (Fig. 4) that similar inclusions occur within this tissue as are found in the developing ova suggesting that the parenchymal tissue may participate in yolk and/or lipid deposition.

Since both polar bodies are formed after fertilization (Okada 1968) it appears that the chromosomes of the ova rest in a diffuse state. The ovum is mature at a diameter of approximately 150 μm and is surrounded by a thin membrane. In the living state the ovum appears pale yellow to yellow-green with the yolk appearing as small refractile inclusions along with several larger oil droplets, which are seen to coalesce in the later developmental stages after fertilization.

Spermatogenesis

The spermatogonia similarly appear in the lateral peritoneum of the septa and parapodial bases as clusters of cells containing varying numbers of spermatogonia (Fig. 5). The spermatogonial nucleus is strongly basophilic containing a great deal of dense chromatin evenly distributed within the nuclear sap while the cytoplasm is reduced to a thin layer around the nucleus. As growth continues the spermatogonial clusters move into the coelomic cavity where sperm plaques, characteristic of polychaetes in general (Okada 1968), are formed. The plaques are composed of numerous cells forming spheres of approximately 15 to 30 μm in diameter (Fig. 6). It seems likely that the increase in plaque size is due to the maturation divisions undergone; however, no distinct division figures were observed. The nucleus of each spermatid now contains knotted chromatin with the cytoplasm barely visible. As chromatin condensation continues, the plaques begin to break up so that at sexual maturity the male's coelomic cavity is filled with individual spermatoozoa (Fig. 7). The mature spermatozoon is of the primative type (Simpson 1962) with a characteristic spherical head measuring 2 to 3 μm in diameter, bearing a rounded acrosomal cap. At the base of the head there appears to be four spherical elements comprising the middle piece which in turn surrounds the base of the flagellum that measures approximately 30 μm in length. The mature spermatozoon is highly active and remains this way in a sea water suspension at 10°C for nearly a day, although the duration of its fertilizing capability has not been investigated.

Spawning

Spawning animals were never observed in the water or on the substrate surface

of their environment, nor were spent animals ever found except in their burrows, thus it was assumed that *L. culveri* spawned within its burrows. This was further substantiated by the fact that young setigerous larvae were collected from within the burrows of the adult. Fortunately several animals did spawn in the laboratory.

With the male there are two methods for sperm emission: (1) The animal's posterior one-third to one-fourth is rapidly lashed back and forth and at the same time a dense stream of spermatozoa is shed through swollen pygidial papillae (Mazurkiewicz, per. comm.). There does not appear to be any rapid and/or violent contraction of the body wall as this occurs. (2) A resting male may also be stimulated to shed spermatozoa by gently prodding the body wall with a smooth probe. In this instance streams of spermatozoa are seen to emerge from both sides of the ventral surface of several segments adjacent to either side of the point of tactile stimulation, presumably through the nephridiopores. In this case a violent contraction of the circular muscles of the body wall is seen.

As is generally the case with female nereids (Clark 1961 and 1965) the ova are shed by dehiscence. The spawning female of *L. culveri* exhibits gentle undulations that rhythmically move down the body from head to tail, while the parapodia are moving fore and aft with a gentle fan-like motion. The freshly shed ova appear on the dorsal surface of the animal adjacent to the base of the parapodia on each segment and are moved distally between the shafts of the setae as these structures are extended and retracted, until the ova drop off onto the bottom of the culture dish. In both sexes, with the cessation of spawning activity, the spent animals usually die within the next 24 hours.

Two definite spawning periods were observed at the Harbor Island population; one encompassed the months of August and September, 1969, the second period was from mid January to mid February, 1970 (Table 1). These dates were arrived at on the basis of the coloration, behavior (spawning) and gamete size of the material collected at these times. The data are not sufficient to definitely establish an annual spawning period, however the variability of the reproductive habits within a single species of nereid is notorious, for example, Dales (1950) cited data in which the breeding periods of *N. diversicolor* are claimed to be anywhere from one to twelve months! In the population of *L. culveri* individuals exhibiting a wide range of ova size, weights and segment counts were collected during a given sampling, indicating that this was a very heterogenous population with regard to individual maturity (Table 1). This heterogeneity could account for an extended breeding season for this polychaete as pointed out by Thorson (1946) in his study of factors affecting the length of breeding seasons in marine organisms.

LARVAL DEVELOPMENT

Early Development

The homolecithal ova of *L. culveri* reach approximately 150 μm at maturity and are demersal, although they regularly contain oil droplets thought to be associated with ova of species of a more pelagic nature (Dales 1950). Upon being

shed into sea water the ova do not develop the thick gelatinous envelope described for other species of the Nereidae, *e. g., Nereis japonica* (Izuka 1908), *N. diversicolor* (Dales 1950), *N. limbata* or *N. megalops* (Wilson 1892). Approximately one hour after fertilization the fertilization membrane was lifted off the surface of the vitellus. Close examination with phase contrast optics at this stage also disclosed the existence of a fertilization cone (Fig. 9) substantiating spermatozoon penetration. At two hours, polar body formation occurred and was identified by a slight flattening of the embryo's animal pole and a clear area appearing beneath the fertilization membrane at this point (Okada 1968). The polar bodies were very small and owing to the yolky nature of the egg they were difficult to detect (Fig. 9). By three hours the first cleavage plane, running diagonally from the animal pole to the vegetal pole, had divided the embryo into AB and CD blastomeres (Wilson 1892 and Fig. 10). The second cleavage furrow appeared approximately sixty to ninety minutes after the two-cell stage, and intersected the first cleavage furrow at right angles to give rise to the four-cell stage (Fig. 11). The four-cell stage remained for approximately sixty minutes before the third cleavage furrow appeared, advancing horizontally, separating the four large blastomeres each into a large and a small daughter cell, the macromeres and micromeres, respectively (Fig. 12). With this last cleavage the micromeres are in fact cut off of one side of the macromeres at an angle to the parent cell thus serving to identify this type of cleavage as spiral, as is most often observed within the Nereidae (Okada 1968).

Gastrulation

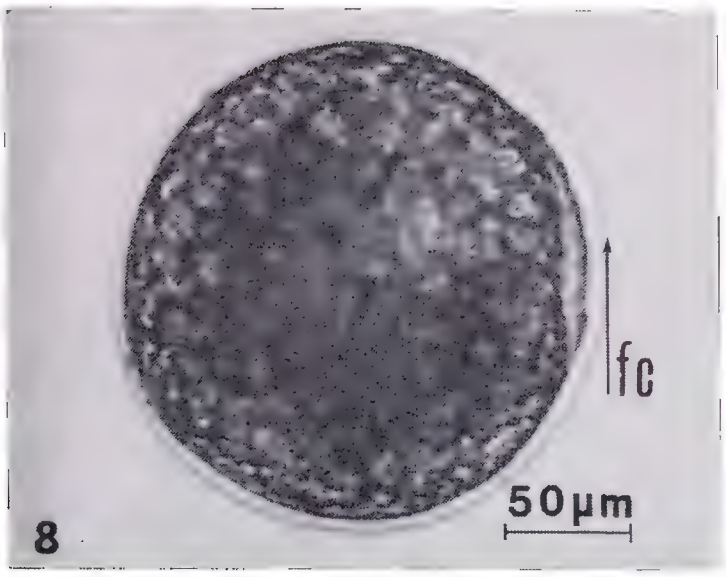
During the next 10 to 12 hours the micromere quartets undergo increased divisional activity, giving rise first to a stereoblastula and then the gastrula, via the epibolic movements of the micromeres (Fig. 13). The macromeres at this stage do not undergo any further divisions due to the inhibitory influence of the large amount of yolk and oil droplets displaced into these cells after fertilization (Okada 1968).

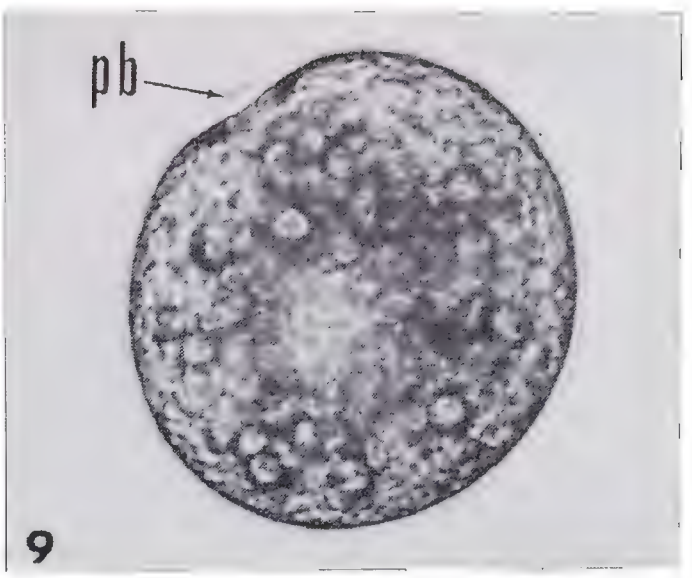
Young Setigerous Larvae

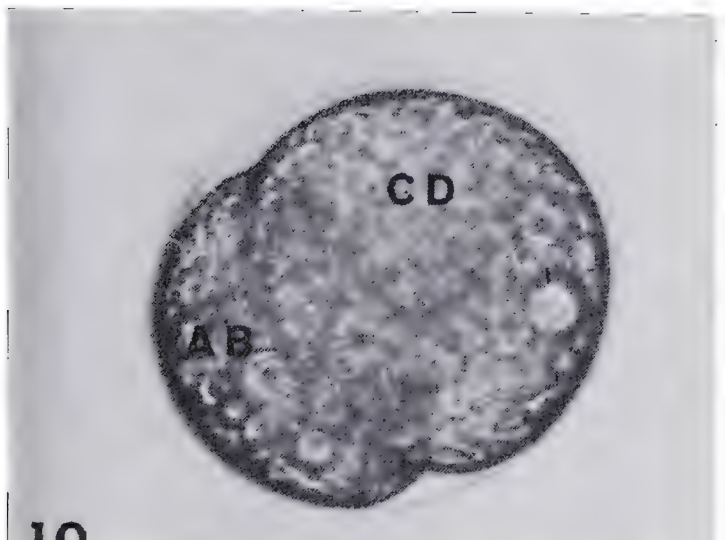
The embryo remains spherical with ciliation and distinct morphological changes difficult to detect for the next two days. At the beginning of the fourth day a slight elongation was observed with the embryo appearing egg-shaped. Definite cephalization occurred with a slight flattening of the anterior end of the embryo, the formation of a posterior border behind the developing eye spots and the appearance of the lateral pigmented areas (Fig. 14). The presumptive parapodial areas appear as slight elevations or buds, three on each side of the embryo. Adjacent to each bud are located the internal setal sacs containing the larval setae, thus establishing this as the 'young setigerous larvae' stage. Individual macromeres as well as oil droplets, are still identifiable within the extensive gut. The embryo now measures 255 μm in length and is slightly motile, although the definite location of the ciliary tracts was not worked out because of the difficulty of accurately observing them with the live material used in this study.

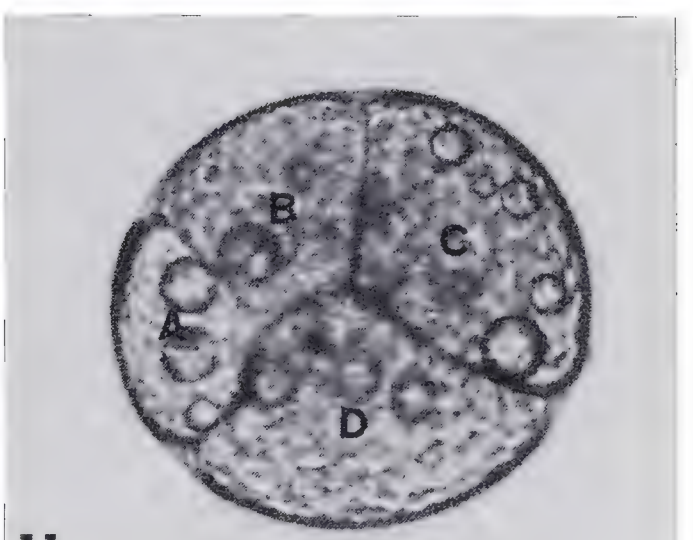
Two Seiger Larvae

At five days the larvae have not grown considerably in length over representatives of the "young setigerous larvae" however the narrower posterior end has









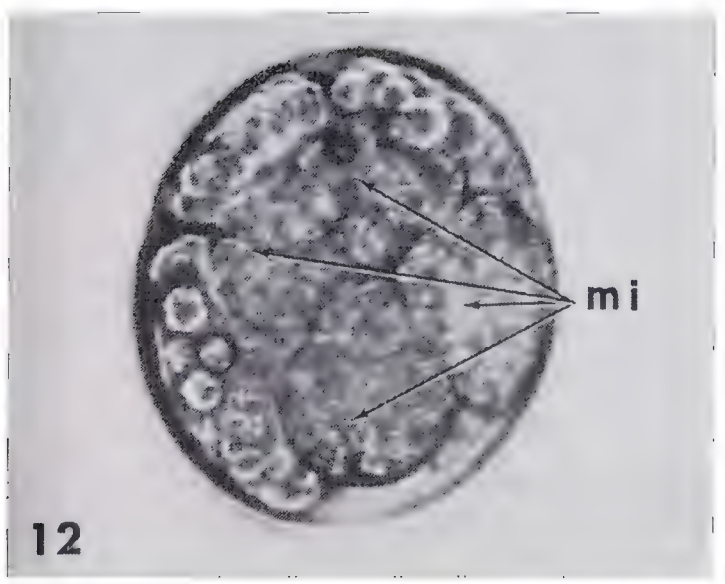


FIG. 8. Ova, one hour post-fertilization, 200 μm in diameter. fc = fertilization cone. 100 X.

FIG. 9. Completion of maturation divisions, two hours postfertilization. pb = polar body. 100 X.

FIG. 10. Completion of first cleavage, with CD blastomere lying above the AB blastomere. 100 X.

FIG. 11. Completed second cleavage into the blastomeres A, B, C, and D. 100 X.

FIG. 12. Completed third cleavage with micromeres (mi) seen lying above and between adjacent macromeres. 100 X.

FIG. 13. Late gastrulation as seen from the vegetal pole with the macromeres still evident. 100 X.

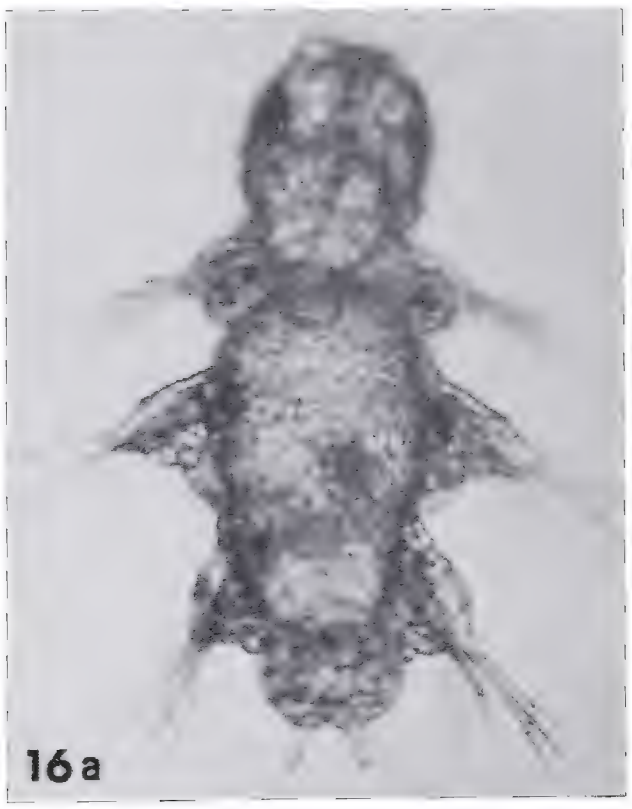


Fig. 14. Dorsal view of a young setigerous larva. 100 X.
Fig. 15. Dorsal view of a larva with two setigerous segments. 100 X.
Fig. 16a. Larva with three equal setigerous segments as seen from the ventral surface. 100 X.
Fig. 16b. Larva with three equal setigerous segments as seen from the dorsal surface. 100 X.

now expanded to a breadth similar to that of the head. The head has undergone further cephalization with the eye spots and lateral pigmented areas now being very prominent (Fig. 15). The head has begun to compress anteriolaterally developing a slight apex anteriorly. The parapodia are now more prominent with setae extending from the first two such structures. The anal cirri can just be made out, appearing as two small buds at the posterior end of the larvae. The pharyngeal area is now located midventrally as a clear area having a median longitudinal cavity, and the gut is still very extensive with the remaining macromeres occupying most of its cavity. The larvae at this stage are now able to crawl upon the bottom of the culture dish with the aid of the parapodial setae. thus the formation of functional musculature has also begun. The larvae are also fully capable of swimming in which instance the parapodia are laid back flat against the body

wall and swimming accomplished via the cilia tracts now seen adajacent to the head and on each segment. Neither the crawling nor the swimming activity lasts for an extended period of time.

Three Equal Setiger Larvae

The week old larvae are now 380 μm in length and possess three well defined though rudimentary parapodia. The setae of each parapodia, homogomph and heterogomph falcigers, emerge from separate neuropodial and notopodial setal sacs. The muscles of these setal sacs are well developed as the parapodia and setae are in a constant state of activity. Cilia tracts are still seen on the head and on each segment. The head has continued its anteriolateral compression so that it is now narrower than the width of a segment and its parapodia (Fig. 16a and b). At the anterior end are now formed the beginnings of the prostomial tentacles while posteriolaterally and adjacent to the eyes are seen two similar processes, the peristomial cirri. The two lateral pigmented areas now form an extensive stripe on either side of the head. The rectal and pharyngeal regions of the gut have become better developed, a pair of simple jaws can be seen and the beginnings of the nephridia can be made out as dense masses lying near the septa of each segment at the parapodial bases. Well defined anal cirri can be seen now to be growing out on either side of the anus. The larvae has now reached the 'three equal setiger' stage. Growth beyond this stage was not observed due to our inability to maintain the larvae beyond this last stage.

DISCUSSION

If there is any one characteristic generally attributed to the Nereidae it is the phenomenon of reproductive swarming (Clark 1961). At specific times during the year, dependent upon the geographic location and the species, polychaetes, normally not particularly gregarious, form dense swarms at the surface of the sea for the purpose of spawning. A definite prerequisite for this swarming act is a modification of the body, producing limbate setae, enlarged eyes, pronounced beading of the dorsal cirri in the male and a sharp division of the body into two or three regions, enabling these normally burrowing polychaetes to become active swimmers (Smith 1958). The modification into the special reproductive form is known as epigamy (Gidholm 1967). The control of the modification into the epitoke within the Nereidae can be shown to be under the control of a hormone or hormones originating from the supra-esophageal ganglion (Clark 1959, 1965; Durchon 1952; Hauenschild 1956b; and Hauenschild and Fisher 1962). The hormone(s) act in a manner analogous to the juvenile hormone of insects in that it maintains the worm in an immature state until its inhibition is lifted by an as yet unknown stimuli. With the inhibition of the cerebral hormone lifted the animal will mature into a sexually ripe individual and metamorphose into the epitoke; however, there must be maintained a low level of hormone(s) to complete gametogenesis and the heteronereid transformation (Clark 1965; Hauenschild 1964). This same hormone(s) is also produced in those species which do not undergo the heteronereid transformation. Hauenschild (1956a) was able to inhibit epigamy in *Platynereis dumerilli* by implanting the supra-esoph-

ageal ganglion of immature *Platynereis massiliensis* a closely related but non-metamorphosing species. Boilly-Marer (1962) has found that repeated injections of aequous extracts of *Nereis diversicolor* ganglion, another non-metamorphosing species will inhibit metamorphosis in decerebrate *Perinereis cultrifera*. Thus it appears that the same hormone(s) controls gametogenesis and the heteronereid transformation within these species and possibly even within the Nereidae.

L. culveri is a non-metamorphosing polychaete that undergoes several changes upon approaching maturity, namely the coloration change, the histolysis of the gut and musculature and the formation of parenchymal tissue. These changes are presumably under the control of a similar hormone(s) as discussed above. This atoquous breeding with accompanying tissue histolysis, as exhibited by *L. culveri*, is apparently the rule among the more than fifty fresh and brackish water nereids (Clark 1961) with only *Nereis chilkaensis*, *N. nouhuysi* (Monro 1931), *Nicon aestuarinus* (Knox 1951) and *Tylorrhynchus heterochaetus* (Okada 1950) undergoing a complete epitokal metamorphosis. *Nereis seurati* (Gravier 1905), *N. megitti* (Monro 1931) and *N. japonica* (Smith 1958) exhibit incomplete metamorphosis while the remaining fresh and brackish water species breed either in the atokous condition or in some instances are viviparous or are thought to be, e.g. *Nereis limnicola* (= *Neanthes lighti*, Smith 1950, 1958) and *Namanereis* (= Lycastis) *quadraticeps* (Johnson 1908).

Regarding the 350 representatives of the family Nereidae (Hartman 1959) the most common form of reproduction generally appears to be epitokal (Reish 1957), while those members inhabiting brackish to fresh water environments are characterized by atokous breeding (Clark 1961). The adults of *L. culveri* (Oglesby 1965 a and b) and *N. diversicolor* (Smith 1955 a, b, c, 1956, 1957) have been shown to be capable of osmoregulation, thus these animals are able to maintain a relatively stable coelomic fluid in which the gametes or larvae, in the viviparous forms, may mature while existing in areas characterized by large salinity fluxuations (Table 1 and Smith 1964a). The ability of *N. diversicolor* and *L. culveri* to survive in fresh water however apparently does not confer any selective advantage to the larvae. Smith (1964b) has shown that cleavage and early larval development are blocked outside the range of ca. 5 to 15 g Cl/L in *N. diversicolor*, and states that populations found outside this range, particularly towards fresh water, are probably non-reproductive. With the similarity of reproduction, development and habitate between *L. culveri* and *N. diversicolor* (Dales, 1950) it can tentatively be stated that the larvae of *L. culveri* probably also exhibit a similar type of salinity tolerance, although further investigation must be undertaken to substantiate this thesis.

Examination of reproduction within the Nereidae reveals basically two types of patterns, the epitokal and the atokal. The pattern within the epitokal forms show a remarkable similarity of detail (Smith 1958). A great dissimilarity is seen with the atokous forms however, ranging from the dioecious, oviparous form of *L. culveri* and *N. diversicolor* (Dales 1950) to the viviparous hermaphrodite as seen in *N. limnicola* (Smith 1950) or the oviparous hermaphrodite, *Platynereis massiliensis* (Hauenschild 1951). These reproductive dissimilarities among the atokous forms warrent their continued study to provide an accurate picture

of the nereid penetration into freshwater environments, a penetration not seen as extensively in any other polychaete family (Hartman 1938; Wesenburg-Lund 1958).

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THE EYES OF WHITE SHRIMP, *PENAEUS SETIFERUS* (LINNAEUS) WITH A NOTE ON THE ROCK SHRIMP, *SICYONIA BREVIROSTRIS* STIMPSON

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ABSTRACT

Several interesting structures are present in the eyes of the white shrimp, *Penaeus setiferus*, including three distinct reflecting layers, a strongly refracting spot in the center of each facet of the cornea, sheaths around the distal ends of crystalline tracts and fibers arising distally from the retinula cells. Suggestions were made concerning the functions of these structures. The distal reflecting layer increases the amount of oblique light collected by ommatidia whereas the proximal reflecting layer serves a protective function back-scattering light which enters the translucent eyestalk. The crystalline tract sheaths appear to serve as light insulators. The retinular fibers are concerned with changes in the shape of retinula cell bodies.

Only the proximal absorbing pigment migrates in response to changes in light intensity in white shrimp eyes. Both the distal and proximal dark eye pigments migrate in the rock shrimp, *Sicyonia brevirostris*. Furthermore, contraction and expansion of two reflecting layers were found in white shrimp eyes.

The white pigment layers are effective diffuse reflectors. They are composed of myriad densely packed granules about 1 μm in diameter whose refractive index is greater than 1.78.

Diffraction images produced by the cornea are not believed to play a role in the formation of superposition images because of the decreased intensity at the level of the rhabdomes and distortion by the optically heterogeneous eye fluid if images leave the crystalline tracts. More important, the structure of the crystalline tracts which might function as light guides supports the contention that no superposition images are formed.

INTRODUCTION

Three species of penaeid shrimp: the white shrimp, *Penaeus setiferus* (Linnaeus); the brown shrimp, *Penaeus aztecus* Ives; and the pink shrimp, *Penaeus duorarum Burkenroad* are of commercial importance in the Gulf of Mexico. They occur in turbid bay and inshore Gulf waters where light penetration is often very poor. Eyes of white shrimp trawled from seven meters depth during daylight

hours with the sun high overhead often glow red when observed, indicating the dark adapted state.

White shrimp are primarily diurnal in habit and brown and pink shrimp are nocturnal as attested to by the nature of daytime and nighttime trawl catches. Brown shrimp are often captured during daylight hours when the sky is heavily overcast (Gunter 1950). Because periods of activity appear to be influenced by light, it is desirable to have an understanding of the structure and functioning of their visual organs. Several studies have been initiated to this end. The present one considers the histological structure of the eyes of white shrimp and confirms and extends Ramadan's (1952) excellent work on *Metapenaeus monoceros*. Also, this study delineates some changes occurring in the eye during light and dark adaptation.

METHODS AND MATERIALS

Microtechnique for preparing white shrimp eyes

White shrimp were collected in the bays and inshore Gulf waters near Port Aransas, Texas, by otter trawl. The animals were stored in tanks with running seawater until needed.

After several hours of light or dark adaptation, the eyes of white shrimp were removed and fixed in either 10 % formalin with a small amount of calcium carbonate, Zenker's fluid or Bouin's fluid for 24 hours. The eyes were maintained under their respective light or dark conditions throughout the period of fixation. All of the fixatives used gave adequate preservation. Fixed eyes were double embedded by Peterfi's celloidin-paraffin technique, cut into sections 10 μm to 20 μm and stained with Mallory's or Masson's triple stains. Better differentiation of tissues was attained by Masson's method.

Absorbing pigment in some sections was bleached to expose underlying structures. Several bleaching methods were tried including the chlorate method, the chromic acid method and the peroxide method (Humanson 1967). The chromic acid method had the greatest success though not all of the dark pigment was removed. This bleaching technique did not remove the reflecting pigment.

No adequate method was found to remove reflecting material without damage to ocular tissues. Immersion of deparaffinized sections overnight in 1 % NH_4OH aqueous dissolved most of the reflecting pigment, but proved destructive to tissues.

In some cases, whole eyes were studied. Eyes fixed in Bouin's fluid or fresh eyes were sliced into thin sections with a razor. Tissues were teased apart and examined by phase contrast.

Light and dark adaptation

White shrimp were light or dark adapted for 2, 3, 6 or 18 hours. Dark adaptation took place in a black room free of light leaks. Shrimp were light adapted in tanks whose white bases and sides offered even brightness from all directions. Six Kenrad F40CW fluorescent lights illuminated the tanks from above.

With the completion of a designated period under light or dark conditions, the shrimp were immersed in scalding water for a few seconds to fix the tissues. The eyes were severed at the stalk and placed into a fixative solution, Zenker's or Bouins fluid, for 24 hours. A sharp scalpel blade was used to split the eye through a vertical plane exposing the pigment layers for low power microscopic examination. The positions of the absorbing and reflecting pigments were noted. This same procedure was employed with the rock shrimp, *Sicyonia brevirostris*.

The possibility of diurnal periodicity in the migration of eye pigments was taken into account. All light adapted shrimp were killed shortly before noon and all dark adapted animals were killed near midnight.

Properties of the reflecting material

The refractive index of the reflecting material was determined and because of the granular

nature of the reflecting layers, the possibility of polarization of light reflected from these layers was examined.

Relatively clean preparations of reflecting granules were obtained by direct smears of the reflecting layers or by separation in sucrose density gradients. A white shrimp was dark adapted for three hours exposing the middle reflecting layer. The shrimp was submersed in near boiling water and the eyes were removed and dissected. Some reflecting material was smeared onto a glass microscope slide. After drying, a drop of immersion oil was placed on the smear together with a cover slip and sealed with ringing solution.

Alternatively, reflecting layers were removed from heat fixed eyes, eliminating as much extraneous tissue as practical. The reflecting material was ground in a tissue homogenizer and suspended in 0.24 M sucrose. A sucrose gradient was set up by layering progressively less dense sucrose solutions in 13 × 100 mm test tubes. Density strata consisted of 0.5 ml of 2.6, 2.4, 2.2, 2.0, 1.8, 1.6, 1.4, 1.2 and 1.0 molar sucrose (Seiji, Shimao, Birbeck and Fitzpatrick 1963, Matsumoto and Obika 1968).

The gradient was allowed to equilibrate for four hours before the suspension of homogenated reflecting tissues in 0.24 M sucrose was floated over the gradient surface. After 24 to 48 hours, larger particles had passed through the gradient leaving a turbid pink layer at the top. The top layer was removed by pipette and placed on glass slides and sealed with ringing solution under a cover slip. Some slides were prepared in which the granules were mounted in immersion oil. Granules in sucrose solution were dried on a slide. The slide was dipped into distilled water to dissolve the sucrose crystals, dried and mounted in oil.

The refractive index of the reflecting granules was investigated by the immersion method. Granules fixed on microscope slides were submersed in liquids of known refractive index and examined by phase contrast. The series of liquids used included sucrose solutions ($N = 1.3 - 1.5$), immersion oil ($N = 1.51$), aniline ($N = 1.58$), quinoline ($N = 1.62$), methylene iodide ($N = 1.74$) and methylene iodide saturated with sulfur ($N = 1.78$).

Diffraction images behind the cornea

To examine diffraction patterns formed by the cornea of the eye, a cornea was removed from a white shrimp eye and cleaned free of other tissues with a cotton swab. Portions of the cornea were mounted on a glass slide with distilled water. The microscope was focussed above the plane of the section and diffraction images which formed were photographed.

OBSERVATIONS

Histology of the eye

The eyes of *P. setiferus* are stalked and subspherical reaching over 8 mm in diameter in adults. Chromatophores are distributed over the dorsal surface contributing to external coloration. The stalk cuticle appears to be somewhat translucent and may well permit light infiltration into the nervous issue and musculature.

The eye can be withdrawn into protective sockets or extended laterally. References in this text to anterior, posterior, lateral, dorsal and ventral apply to the eye in the extended position. Measurements of diameters refer to the longest line in an anterior-posterior direction across the eye. Other dimensions are given for structures located in central facets of an eye six mm in diameter unless otherwise stated.

The Ommatidium (Fig. 1)

Each ommatidium is enclosed distally by the cornea which is secreted by two corneagenous cells. The crystalline lens is produced by four cells and itself is a

FIG 1

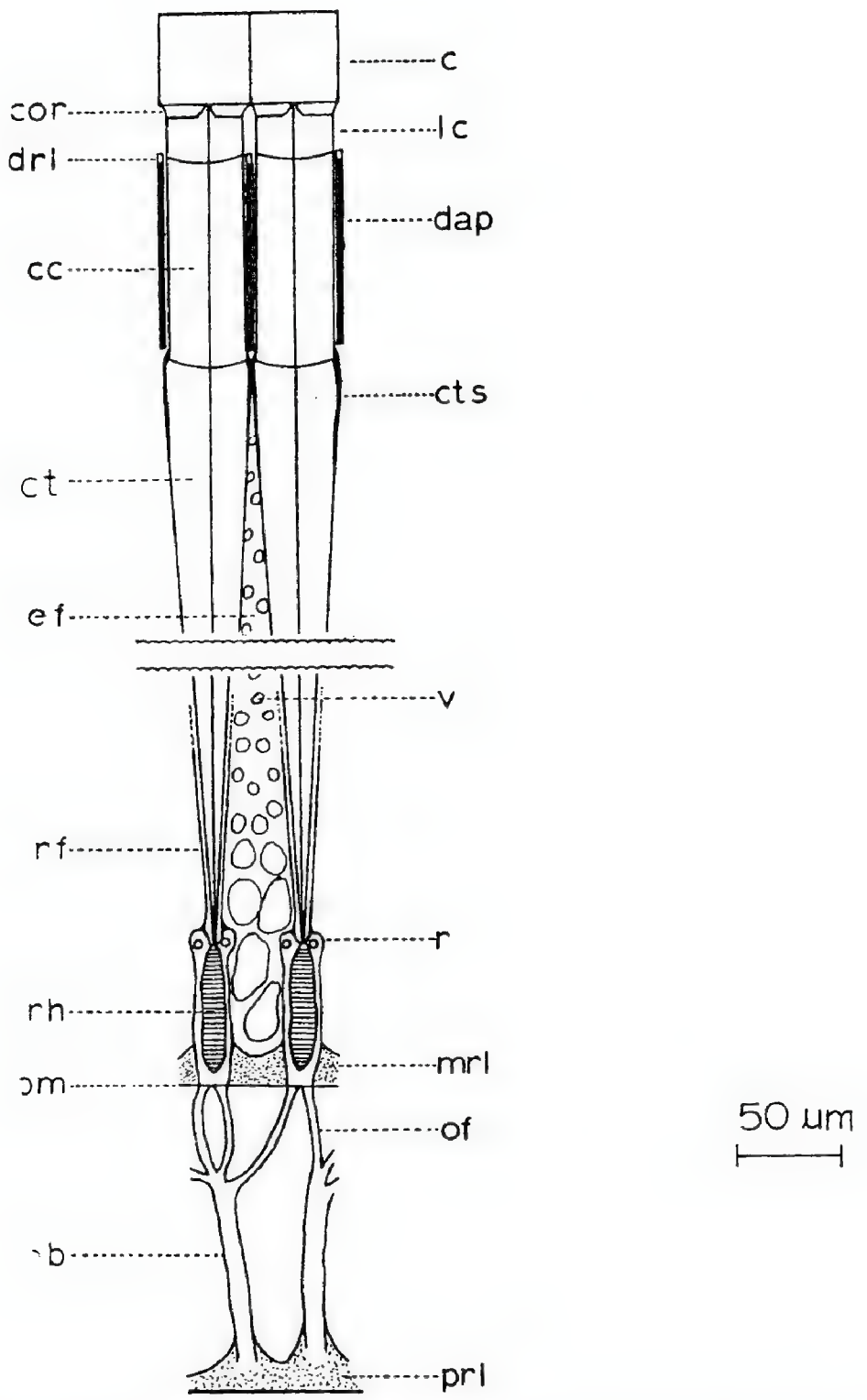


FIG. 1. Longitudinal section through two ommatidia. The crystalline tracts could not be drawn in scale. The break equals 750 µm. bm, basement membrane; c, cornea; cc, crystalline lens; cor, corneagenous cell; ct, crystalline tract; cts, crystalline tract sheath; dap, distal absorbing pigment; drl, distal reflecting layer; ef, eye fluid; lc, lens cell; mrl, middle reflecting layer; ob, primary optic fiber bundle; of, primary optic fiber; prl, proximal reflecting layer; r, retinula; rf, retinular fiber; rh, rhabdome; v, vacuole.

composite of four sections. The crystalline tract tapers gradually until meeting the distal end of the rhabdome. Like the lens, the crystalline tract is divided into four segments. The rhabdome is fusiform and surrounded by seven retinula cells which merge into nerve fibers beneath the fenestrated basement membrane.

Distal absorbing and reflecting pigment is incorporated in cells around the lens. The retinulas contain absorbing pigment which migrates into primary optic nerve fibers below the basement membrane. Cells with reflecting material fill the interstices between the bases of the rhabdomes. A third layer of reflecting material is fixed in the region distal to the lamina ganglionaris where the primary optic nerve bundles terminate. The spaces between ommatidia are filled with an appreciable amount of optically heterogeneous fluid and form the eye cavity.

The Cornea (Fig. 4A)

The tough outer cuticle is supportive, allowing the eye to maintain turgor, and transparent, serving as a cornea. Its outer surface is smooth. The cornea is divided into square facets separated from each other by refringent borders. A highly refringent dot 5 μm in diameter marks the center of each facet. The spot does not penetrate to the distal corneal surface and is not seen in fixed tissue.

Facets vary in size from the center of the eye to the periphery and cause irregularities in the symmetry of the surface pattern. A series of measurements was made of the size of facets beginning from the center of the eye, skipping intermittently toward the stalk. The width of the facets measured decreased as follows: 42, 40, 35, 21, 17 and 15μm. The thickness o fthe cuticle was 40 μm.

Histochemically, the thin outer layer of the cornea differs by staining red with Masson's trichrome stain whereas the remainder stains green. Numerous chromatophores ornament the cornea dorsally.

The Corneagenous Cells (Fig. 2A)

The cornea is secreted by two corneagenous cells which are probably modified epidermal cells (Waterman 1961). The two cells form a square of the dimensions of their facet and are appressed to the underside of the cornea. Each cell contains a large oval nucleus. Unlike *Metapenaeus* (Ramadan 1952), the cells in neighboring facets are not all oriented in the same direction. The outer edges of the cells narrow slightly and a depression, the shape of a truncated four sided pyramid with a narrow extension, penetrates the base of the cells.

The Crystalline Lens Cells (Fig. 2B)

Four cells give rise to the crystalline lens (Waterman 1961). These are shaped distally to fit between the corneagenous cells. Each of the cells possesses a nucleus which is bent at right angles and fits in the corner. The four cells together form one convex base. In ommatidia nearer to the stalk, the base of each cell is convex forming four bulges which become more pronounced in facets adjacent to the stalk. This probably represents a developmental phase in the production of the lens. These cells are approximately 21 μm thick and stain red with Masson's.

The Crystalline Lens (Fig. 2C)

The crystalline lens is elongate and square in cross section. It is concave distally and convex proximally. The lenses near the eye stalk have four concave depres-

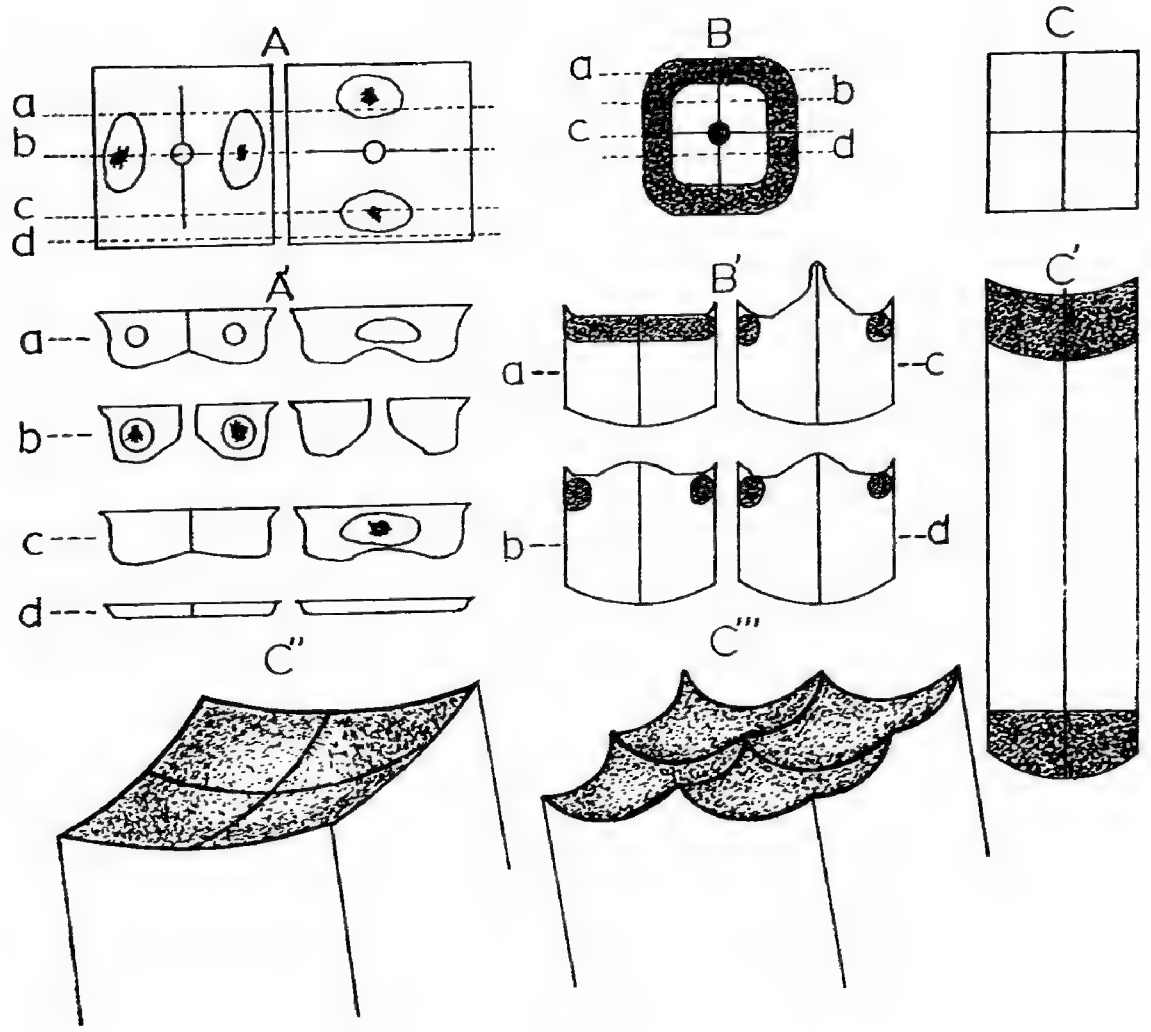


FIG. 2

A—Top view of four corneagenous cells each bearing an oval nucleus. Each pair of cells is perforated centrally.

A′—Vertical sections through A.

B——Top view of four lens forming cells. A nucleus bent at right angles is present in the outer corner of each cell.

B′—Vertical sections through B.

C—Top view of crystalline lens showing the division into four segments.

C′—Vertical section through the lens. Refractile bands which stain dark red with Masson's trichrome appear at either end.

C″—Distal end of lens in central facets.

C″ ′—Distal end of lens in peripheral facets.

sions into which the lens forming cells fit and four convex bulges proximally. Lenses near the center of the eye are approximately 107 μm long. They are differentiated into three zones by their staining affinities. A distal and proximal band stain deep red while the largest central portion stains poorly with Masson's.

The Crystalline Tract (Fig. 3A)

Ramadan (1952) called this structure part III of the crystalline lens. The term crystalline tract has been widely used for these long thread-like elements which may possibly function as light guides. The crystalline tract distally is shaped to fit the base of its lens. Adjacent tracts are in contact before tapering. A dark stain-

ing sheath which continues from the base of the lens surrounds the tracts and fades away as the tracts separate (Fig. 5D). The tract is square in cross section and formed of four square subsections; it is very elongate and tapers to a fine thread where it meets the rhabdome. The crystalline tracts measure over a millimeter in length and stain red in Masson's.

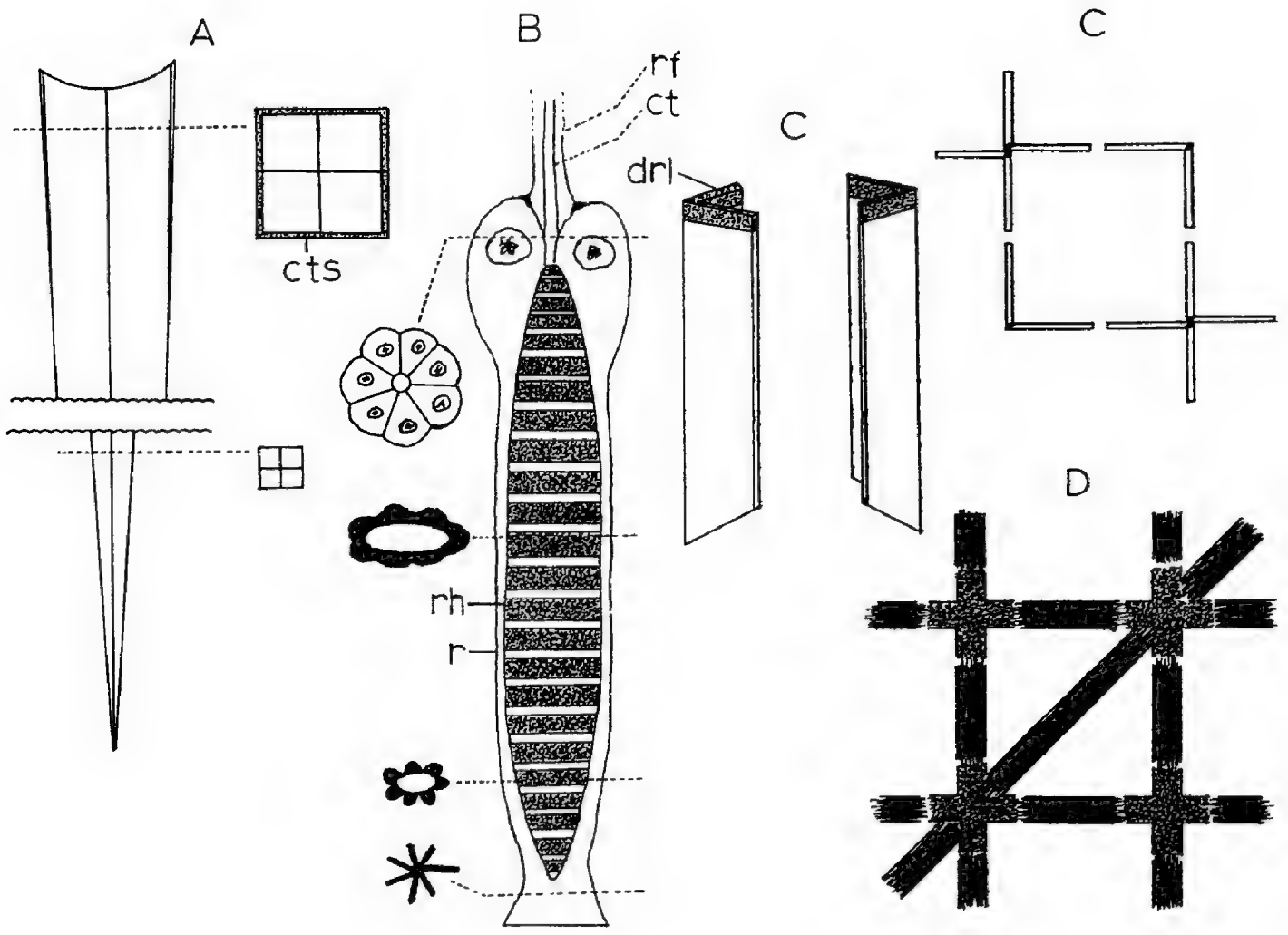


FIG. 3

A—Crystalline tract and sections cut at two levels showing division into four segments. A sheath surrounds the tracts distally. The tract which reaches 1 mm in length is broken to maintain proportions.

B—Fusiform rhabdome surrounded by seven retinula cells. Sections are cut through four planes. Striations of rhabdome are probably due to microvilli projecting from retinula cells forming rhabdomeres. Fibers arise from the retinula cell bodies distally.

C—Two distal pigment cells almost entirely filled with dark pigment granules except for the distal extremity.

C′—Two distal pigment cells of a single facet and half of four adjacent pigment cells are arranged to form a complete enclosure around the lens.

D—The reticulate basement membrane composed of numerous fibrils forming a lattice work with bracing diagonal strands. The corners have a different consistency and appear as crosses.

ct, crystalline tract; cts, crystalline tract sheath; drl, distal reflecting layer; r, retinula cells; rf, retinular fiber; rh, rhabdome.

The Rhabdome and Retinula Cells (Fig. 3B)

The rhabdome is a fusiform body, oblong in cross section. A series of transverse striations can be seen in longitudinal section.

Seven retinula cells adhere to the rhabdome. The cell body, a protuberance containing the nucleus, extends distally and a fiber arises from each cell body, passing through the eye fluid alongside the crystalline tract; the distal connection of the fiber was not found. The retinula cells elongate in juxtaposition with the rhabdome and gradually narrow giving rise to primary optic nerve fibers beneath the basement membrane. The distance from the top of the retinula cells to the basement membrane is 90 μm; the retinulas stain red in Masson's.

The Basement Membrane (Fig. 3D)

The basement membrane is a reticulate structure crossed diagonally by bracing strands. The main strands of the grid are themselves composed of many fibrils which become very dense near the points of intersection, giving the appearance of crosses. Retinula cells are perched on these crosses. The membrane has a mesh about 12 μm wide and stains red with Masson's. The crosses stain a much deeper red. This fenestrated membrane lends itself to free communicattion through the membrane while separating and supporting different optic elements.

The Distal Pigment Cells (Fig. 3C)

Two pigment cells bent at right angles enclose diagonal corners of almost the entire length of the lens, tapering to a point proximally. One arm of each cell covers one half of a side of the lens such that the two cells of the lens and parts of pigment cells from the four adjacent lenses form a complete pigment enclosure. This is better understood by examining Figure 3C. A long nucleus in the corner traverses the length of the cell.

The distal ends of the cells contain reflecting pigment granules forming a layer about 5 μm thick. The remainder of the cell is dark with absorbing pigment. Outwardly these cells form a reflecting grid (Fig. 4B).

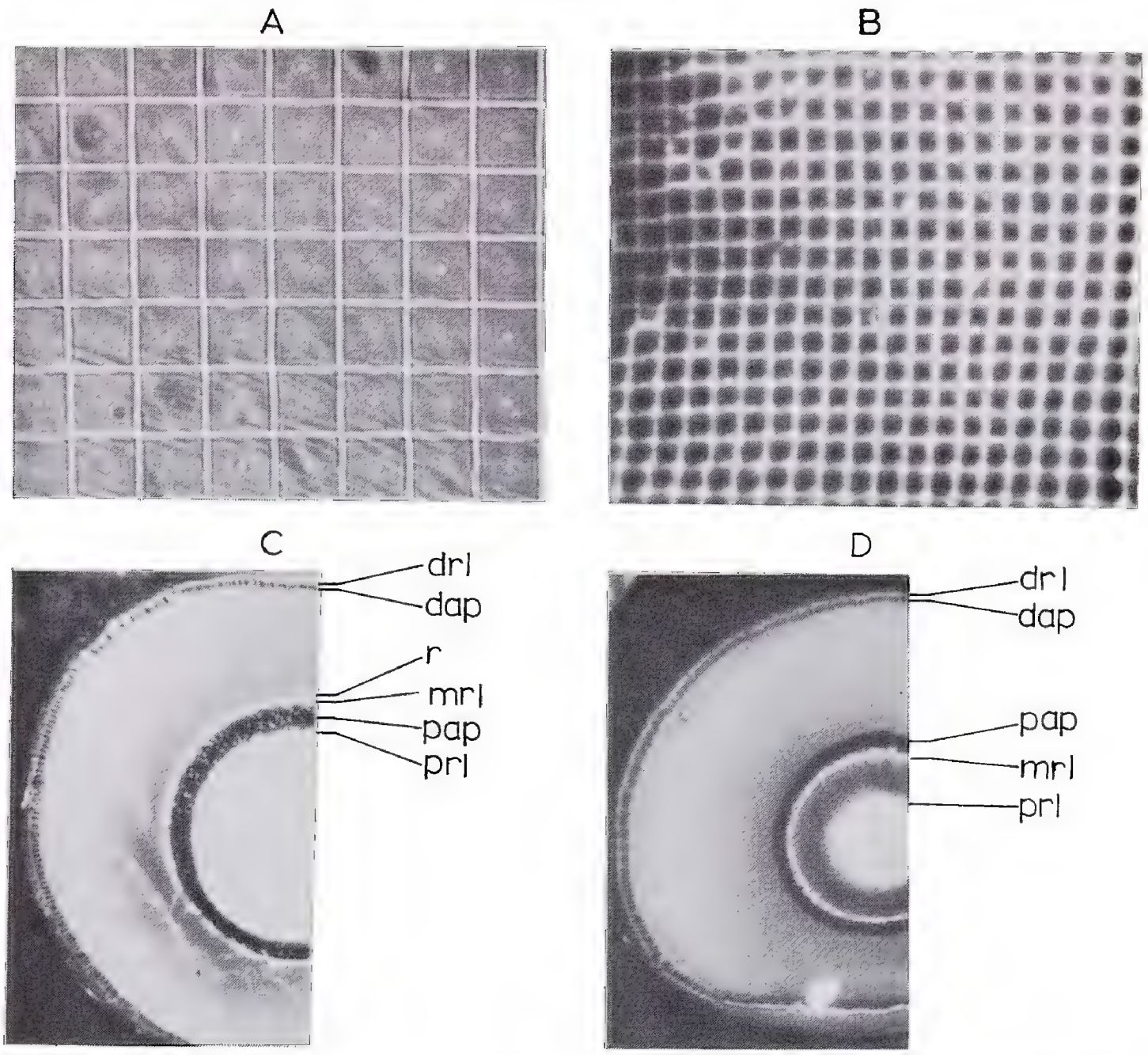
The Proximal Absorbing Pigment

Retinula cells contain the proximal absorbing pigment. This pigment can migrate through the primary optic fibers darkening the region between the basement membrane and the lamina ganglionaris. Some dark pigment always remains in the optic fibers.

The Middle Reflecting Pigment

The middle reflecting layer fills the interstices between the bases of the rhabdomes. It was described as being cellular in *Metapenaeus* (Ramadan 1952), but these cells could not be seen in *Penaeus* for want of a suitable method of removing the reflecting material without injuring tissues.

FIG. 4



A—Phase contrast view of cornea focussed just proximal to the epicuticle. Each facet is 40 μm wide and bears a refringent spot about 5 μm centrally. Facets are demarcated by highly refractive borders.

B—Distal reflecting layer removed from eye and photographed with oblique surface illumination. A lens is set in each opening of the grid which is approximately 40 μm wide.

C—Section through eye (6 mm in diameter) of white shrimp dark adapted for three hours. The proximal absorbing migrated into the primary optic fibers exposing the middle reflecting layer.

D—Section through eye (6 mm in diameter) of white shrimp light adapted for two hours. Absorbing pigment migrated into the retinula cells covering the middle reflecting layer, dap, distal absorbing pigment; drl, distal reflecting layer; mrl, middle reflecting layer; pap, proximal absorbing pigment; prl, proximal reflecting layer; r, retinula cell layer.

The Proximal Reflecting Layer

The proximal reflecting layer is fixed above the region of the lamina ganglionaris. Unlike that described in *Palaemonetes* (Welsh 1930 and Kleinholz 1936), it constitutes a well-defined layer which does not migrate to the middle reflecting layer in the light adapted state.

The Eye Cavity

The fluid filled spaces between the various optic elements constitute the eye cavity. This cavity is minute between the corneagenous cells and lenses. It is confined to the corners between tracts distally and increases as the crystalline tracts taper. The fluid medium may contain mucoprotein which is denatured when heated or fixed and characteristically stains green in Masson's. Stained tissue sections show that the fixed eye fluid is highly vacuolated with dense aggregations of vacuoles proximally.

Pigmentary changes during light and dark adaptation in the eyes of Whie and Rock shrimp

The pigment layers in the light adapted eye of the white shrimp *P. setiferus*, were situated as follows: the distal absorbing and reflecting layers enveloped the crystalline lens, proximal dark pigment filled the retinula cells forming a dark shield around the rhabdomes (some of this dark pigment remained in the primary optic fibers), the middle reflecting pigment was compacted at the base of the rhabdomes but above the lamina ganglionaris (Fig. 4C). The relative positions of the reflecting layers did not change whether the animals were light adapted for 2, 3 or 18 hours.

Dark adaptation in the white shrimp involved the shifting of positions of only one pigment layer, the proximal absorbing pigment, and expansion and contraction of the middle and proximal reflecting layers, respectively. Dark pigment in the retinula cells retreated into primary optic fibers in eyes that were dark adapted for three and six hours and killed near midnight (Fig. 4D). The middle reflecting layer was uncovered and the rhabdomes and retinulas were fully exposed to any light entering the ommatidia. No changes were evident in the distal pigments. During the light-adapted phase, the proximal reflecting layer extended distally around the primary optic fiber bundles, but, in no case, reached the middle reflecting layer. The proximal layer increased in thickness as measured with an optical micrometer becoming slightly more diffuse (Table 1 and Fig. 5B). On the other hand, the middle reflecting layer contracted during light adaptation. During dark adaptation, just the opposite situation obtained (Fig. 5A). The proximal reflecting layer contracted and the middle reflecting layer expanded. In each instance, the proximal boundary was fixed, and there was no exchange of reflecting material between the layers. The results of fluorometric assays indicate that there was no change in the amounts of pteridines present in

TABLE 1

Thickness of reflecting layers during light and dark adaptation (in μm).

Reflecting layer	Dark adapted one hour	Light adapted one hour
Distal	23	26
Middle	79	57
Proximal	125	216

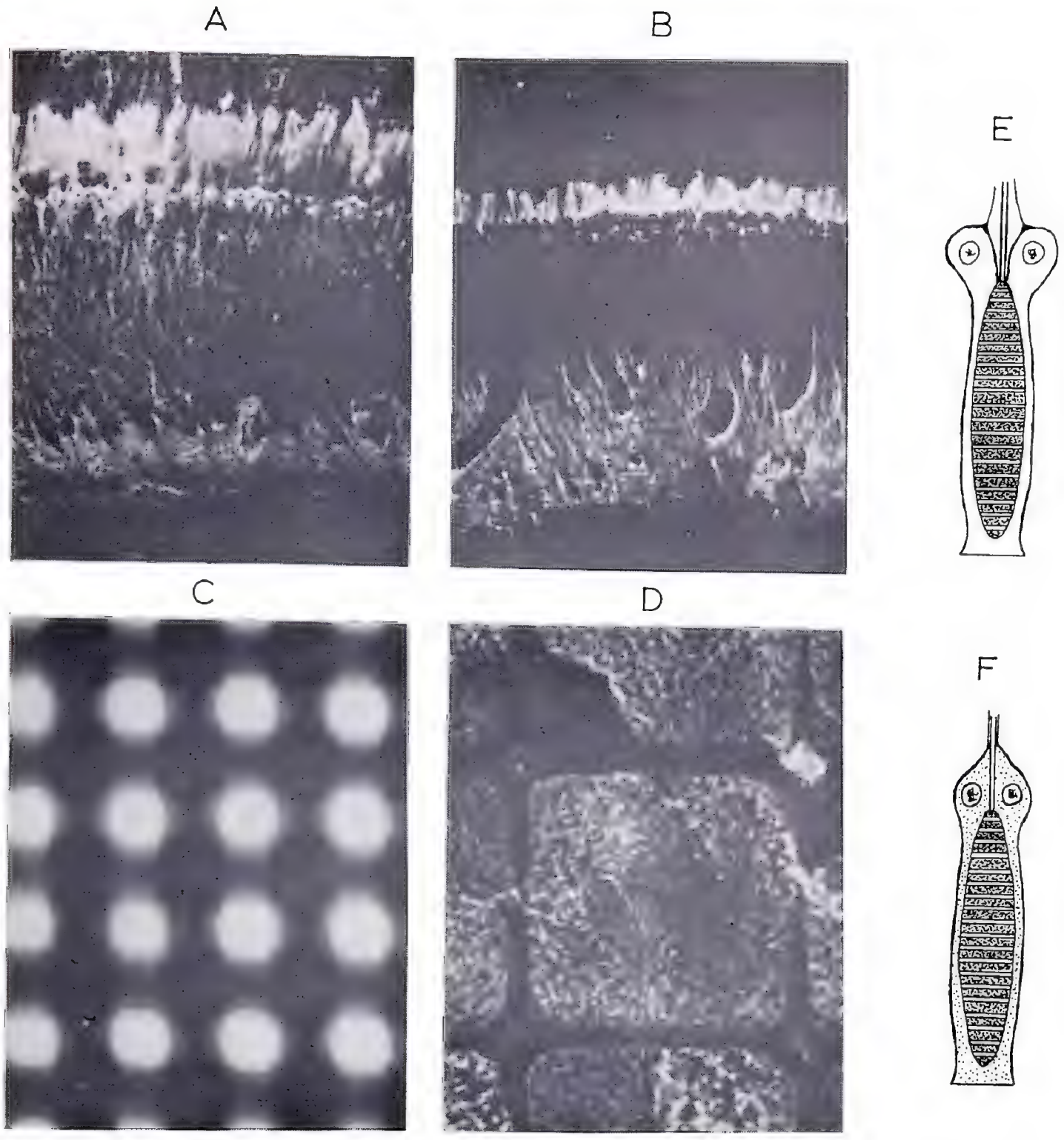


FIG. 5

A—Section through middle and proximal reflecting layers under dark field illumination from eye dark adapted one hour. The middle layer is expanded (79 μm) while the proximal layer is contracted (125 μm).

B—Same as A from eye light adapted for one hour. Just the opposite occurs, the middle layer is contracted (57 μm) and the proximal layer is expanded (216 μm).

C—Diffraction images formed behind a cleaned fresh cornea under bright field with condensor adjusted to admit only axial rays. Different orders of constructive interference move away from each facet in four directions focusing above the cornea.

D—Cross section through distal end of crystalline tract with dark staining sheath (40 mm).

E—Longitudinal section through rhabdome and retinula cells in dark adapted state. The retinula cells bodies are distended and absorbing pigment has migrated into the primary optic fibers.

F—Same as E in light adapted state. Retinula cell bodies are filled with dark pigment and stretched distally around the base of the crystalline tract.

the middle and proximal reflecting layers during light and dark adaptation (Zyznar and Nicol 1970).

A rather different mechanism for light and dark adaptation was found in the rock shrimp, *Sicyonia brevirostris*. Pigment movements in rock shrimp eyes are similar to those of white shrimp except that the distal absorbing and reflecting pigments are not stationary. In the dark adapted state, all pigments are positioned as in white shrimp. The distal pigments, in light adapted eyes, in the dorsal region of the eye and in facets near the eye stalk, migrate proximally toward the rhabdomes. This type of pigment migration is common in other crustaceans described except that only portions of the eyes respond in such a manner.

Changes in the shape of the retinula cells were discovered in white shrimp eyes as they became light or dark adapted. The nucleus bearing cell bodies of retinula cells were greatly distended in the dark adapted eye (Fig. 5E). In light adapted eyes, the distal parts of the cell bodies were compressed against the crystalline tract appearing as a wedge in longitudinal section (Fig. 5F). Fibers, whose distal attachments could not be traced, arise from the cell bodies and apparently stretch the retinulas over the tracts.

Properties of the reflecting material

The three reflecting layers examined with transmitted light were brown and hardly distinguishable from absorbing pigment, but looked white and glowed brightly under dark field illumination. The layers were formed from many round granules about 1 μm in diameter which did not polarize light individually or as a layer. Untreated reflecting granules separated by either of the methods described did not appear different than the granules in histological sections. The refractive index of the granules determined by the immersion method was greater than 1.78. Granules began to fade from sight in methylene iodide saturated with sulfur. The reflecting material is composed chiefly of pteridines and probably some purines (Zyznar and Nicol 1970).

Diffraction images behind the cornea

Focussing above the plane of a cleaned section of cornea, different orders of constructive interference could be seen as bright spots emerging from each side of a facet (Fig. 5C). The images became dimmer and finally faded at levels farther from the cornea. The total diffraction image formed by many facets as it appeared at low magnifications was two bands of light at right angles which intersected at the axial facets.

DISCUSSION

The eyes of the caridean shrimp, *Palaemonetes vulgaris* and *Palaemon varians*, were described by Welsh (1930) and Debaisieux (1944), respectively; the structure of the eyes of the penaeid shrimp, *Metapenaeus monoceros* was worked out by Ramadan (1952). Several important anatomical differences were present in the eyes of white shrimp, *Penaeus setiferus*.

The cornea of the white shrimp eye possesses a highly refringent spot about

5 μm in diameter in a facet 40 μm wide. This spot does not penetrate the epicuticle distally and meets an extension of the four lens forming cells proximally.

The term crystalline cone is inappropriate for the lenses of white shrimp since each lens is quadrilateral in cross section throughout its length and does not taper noticeably. The lenses are demarcated by three zones of different refractivity as seen in preparations of fresh tissues. Sections stained with Masson's indicate higher concentrations of protein at both ends of the lenses.

The crystalline tracts are extremely long measuring over 1 mm in ommatidia 1.25 mm. Their distal ends are wider than the lenses and in contact with each other. Such an arrangement would preclude the tracts functioning as light guides because they would not be separated by media of lower refractive index. Dark staining sheaths surround the tracts distally (Fig. 5D) and disappear as the tracts taper and are separated by eye fluid. Though the refractive index of the sheaths is not known, their location on the tracts suggests the role of light insulator.

In *Palaemonetes*, fibrils extend from distal pigment cells to the retinulas. These were postulated to function as myofibrils whose contraction was responsible for the migration of the distal pigment. A fiber extends distally from each retinula cell in white shrimp eyes. In this animal, the distal pigment is stationary. The retinula cell bodies are distended and unpigmented in the dark adapted state. Under lighted conditions, the cell bodies are stretched and appressed to the crystalline tracts proximally. Dark pigment moves into the retinulas covering the rhabdomes and proximal portions of the crystalline tracts. Though not verified, the stretching of retinula cells appears to be due to contraction of the fibers.

The reflecting layer of Palaemonetes has distal and proximal processes which migrate to and from the main reflecting mass. These processes correspond to the distal and proximal reflecting layers of Penaeus, but differ in several important respects. The three layers of Penaeus are distinct units; in numerous preparations, no processes were seen connecting them. The only point of juncture is found at the margin of the eye stalk where the different layers merge. The distal layer is symmetrical forming a square grid around the outer portion of the lenses and is stationary. The distal processes of *Palaemonetes* lack such symmetry and migrate alongside the crystalline tracts during changes between the light and dark adapted states. In *Palaemonetes*, processes of reflecting material migrate beneath the basement membrane in the light adapted state (Kleinholz 1936) whereas, in the white shrimp, the middle and proximal reflecting layers remain separate though expansion and contraction of these layers do occur as described previously. The amount of reflecting material present in each layer does not change during light or dark adaptation.

The structure and composition of the distal and proximal layers are suggestive of the role they play in vision. Like the middle layer, the two other reflecting layers are composed of myriad granules whose size, density of packing and refractive index makes them favorable as diffuse reflectors of white light. It is of interest to note that the pteridine reflecting granules of white shrimp and guanine employed in other reflecting systems have similar and high refractive indices near 1.8.

The distal reflecting layer forms a square grid positioned at the distal ends of

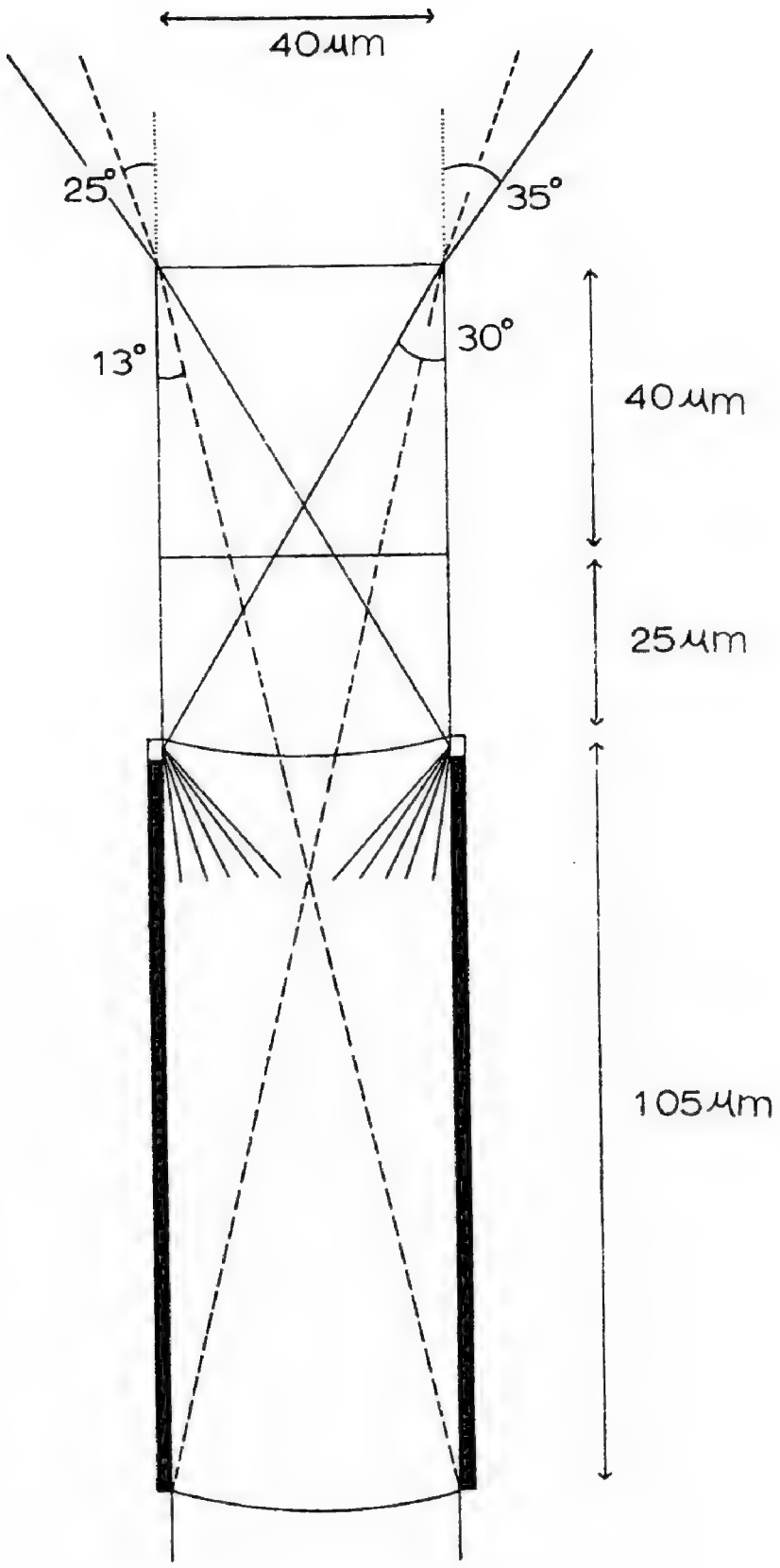


FIG. 6

FIG. 6. Increased acceptance of oblique light by the distal reflecting pigment. A refractive of $n = 1.5$ was used for the cornea and lens. The external medium is seawater $n = 1.35$. If the dark pigment is effective in absorbing some or all of the light incident upon it, only rays incident at less than 15° to the normal to the cornea can penetrate the ommatidium. The distal reflecting layer increases the light collecting ability of the ommatidium by reflecting light incident at up to 35° to the normal to the corneal surface.

the lenses. Such a reflecting layer would increase the amount of oblique light penetrating individual ommatidia (Fig. 6). To animals inhabiting a turbid environment, any system which enhances the collection of light by the eyes is at a premium. The distal layer would increase the amount of light from a point in the visual field reaching near axial ommatidia and increase the number of ommatida viewing the point. The distribution of primary optic fibers from adjacent ommatidia in optic fiber bundles leading to the ganglion layer in the eyes of Limulus is suggestive of lateral inhibition (Kuiper 1962). A similar arrangement of primary optic fibers is seen in white shrimp. Lateral inhibition could prevent transmission of the stimulus by off axial ommatidia while enhancing the light collecting ability of axial facets.

The proximal reflecting layer appears to serve a protective function. The eye stalk is translucent and probably permits the entrance of light into the nerve layers of the eye. The primary optic fibers are continuous with retinula cells and might themselves be photosensitive. Two mechanisms shield the primary bundles. First, some dark pigment remains in the primary optic nerve fibers during light adaptation. Second, the proximal reflecting layer expands enveloping the primary fiber bundles with reflecting granules. Light penetrating the stalk is back scattered at the lamina ganglionaris.

Interommatidial spaces are filled with an optically heterogeneous fluid which forms a large part of the volume of the eye. Fluid removed from fresh eyes with a hypodermic needle or a finely drawn glass pipette was found to contain large numbers of oil-like droplets which refract light strongly within the eye fluid. Nicol and Attaway (unpublished) found that the eyes of white shrimp contained an average of 3.5% cholesterol dry weight. Myelin coatings of nerves and the eye fluid are possible sites of the cholesterol.

Burtt and Catton (1962) suggested an alternate superposition theory based on the discernment of diffraction images. At different levels within the eye, images result from constructive and destructive interference due to diffraction in each facet as light enters the cornea. Such diffraction images were supposed to relay useful information.

Diffraction images do form behind the cornea of white shrimp. Successive orders of constructive interference become less intense and, finally, cannot be seen. The distance from cornea to the rhabdomes in adult white shrimp is greater than 1 mm, casting doubts that useable diffraction images could be formed at this level. Secondly, the images would be further distorted by optically heterogeneous eye fluid should they pass outside the crystalline tracts. More likely, the structure of the tracts indicates a light pipe function and no superposition images are formed.

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FISH SPECIES DIVERSITY INDICES AS INDICATORS OF POLLUTION IN GALVESTON BAY, TEXAS[1,2,3]

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ABSTRACT

Fish species diversity indices (natural bels/individual) calculated for both fish weights and numbers from trawl collections were found to be useful indicators of environmental and pollution stress in Galveston Bay, Texas. Diversity values ranged from 2.2 in the Texas City-Galveston area to 0.02 in the Houston Ship Channel. Thus it is demonstrated that the concept of using species diversity to indicate adverse water quality conditions is applicable to the higher trophic levels of an estuary.

Significant differences were detected in diversity between areas of the bay within each sampling period except in winter as well as between seasons. Also, significant differences between the weight and number indices existed, indicating that both biomass and numbers of organisms should be utilized when studying the diversity of higher trophic levels.

Correlation of diversity with percent waste water indicated that those areas receiving the greatest amounts of effluents and toxic materials (up to 86 % effluent by volume) exhibited the lowest mean annual diversities. Fish diversity in the Houston Ship Channel above Baytown, Texas can be used to predict diversity in the bay because of the linear relationship between distance and dilution of the ship channel effluent (19 % effluent by volume calculated for Bolivar Roads).

Sampling throughout the system indicated that the fish populations could be divided into somewhat separate communities, each structured as a response to environmental and pollution stress. In those areas receiving the greatest stress, the bay anchovy, *Anchoa mitchilli*, was the dominant species. These same areas also supported the fewest numbers of large individuals.

INTRODUCTION

Pollution of estuaries has become a major concern in recent years because of degradation of water quality for domestic, industrial and recreational uses. Studies

[1] This work was done at The University of Texas Marine Science Institute at Port Aransas.
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[3] Contribution number 10, Pamlico Marine Laboratory, N. C. State University.

of pollution effects on aquatic life have taken many approaches. among these being the determination of species diversity, with a species diversity index based on one or more trophic levels used as a tool to assess adverse water quality conditions.

Doudoroff and Warren (1957) stated that there was more published information on the environmental requirements of fish than on the requirements of any other group of aquatic organisms, with the exception of a few commercially important invertebrates. In spite of this, the use of fish as indicators of pollution has received less attention than other major plant and animal groups. microscopic and macroscopic.

There are few published accounts of studies using fish diversity as a pollution indicator. The great difficulty of adequately sampling fish populations with the standard methods of collection, coupled with the great mobility of most fishes, has probably precluded the use of fish for such studies.

The literature indicates that in theory and with actual data. species diversity indices can be used to indicate environmental and pollutional stress. Little work has been accomplished with fish diversity in this regard. although studies using fish have provided information about water quality for many years. The complete absence of fish from areas receiving domestic and industrial wastes was used as an indication of grossly polluted waters by Katz and Gaufin (1953). Tsai (1968) studied the effects of chlorinated sewage effluents on fishes in the Patuxent River. The results indicated that diversity was seriously reduced immediately below the effluent outfalls and increased as distance from the source increased, with a species shift occurring downstream. Armstrong *et al.* (1970) showed similar results in San Francisco Bay.

As a part of the Texas Water Quality Board's extensive Galveston Bay pollution study (Carter 1970; Copeland and Fruh 1970), the fish populations of the bay were sampled with an otter trawl to establish fish species diversity indices to indicate the ecological quality of Galveston Bay areas. These diversity indices could then later be used as a tool in assessing pollution effects. The sampling periods were 18 to 27 February 1969; 15 to 24 April 1969; 14 to 18 July 1969; and 14 to 17 October 1969.

MATERIALS AND METHODS

Description of Study Area

The Galveston Bay estuarine system, located on the southeast Texas coast, is composed of Upper and Lower Galveston Bays, Trinity Bay, East Bay and West Bay. The total bay system has about 300 miles (483 km) of shoreline and a surface area of 334,000 acres (135,170 ha) or about 520 square miles. Water depths in the bays range from 0.5 to 3 m, averaging about 2.2 m, and giving a total volume of water at mean low tide of three billion m^3 (Masch and Espey 1967).

One of the major characteristics of the bay system is the series of dredged channels and accompanying shallow spoil banks and islands. These channel and spoil areas include the Intracoastal Waterway (4 to 5 m), the Houston Ship Channel (11 to 13 m), the Texas City Channel (11 m) and Dike, and numerous other small boat channels around the entire bay shoreline (Lankford and Rogers 1968).

The bay system receives its major source of freshwater input from the Trinity River, which flows into Trinity Bay, and from the San Jacinto River, which flows into the northwestern part of Upper Galveston Bay. Additional freshwater is contributed via the Intracoastal Waterway and the numerous bayous which drain secondary lakes and bays and adjacent marshes. The Trinity River contributes between five and six million acre-feet (6 and 7.2 billion m^3) of freshwater per year, while the San Jacinto River has an annual average discharge of about 700,000 acre-feet (840 million m^3) (Lankford and Rogers 1968). Copeland (1966) calculated that, since 1959, Galveston Bay has received an average annual freshwater contribution of 20.5 acre-feet per surface acre (62,500 m^3/ha).

The Galveston Bay complex is the largest and one of the most important estuarine systems, both economically and ecologically, of all the bays on the Texas coast (Curington *et al.* 1966; Masch and Espey 1967). Because of its large acreage and variety of habitats, the bay provides nursery grounds for over 80 % of the poundage taken as fishery products in the Gulf of Mexico adjacent to the Texas coast (Curington *et al.* 1966).

The sampling stations established for this study were located throughout the bay system (Fig. 1) and included a variety of different habitats, known nursery areas, major channels and areas suspected of being grossly polluted. All major areas of water exchange were sampled. U. S. C. & G. S. Chart 1282 may be consulted for detailed data concerning sampling stations.

Sampling Procedure

The stations indicated in Figure 1 were sampled seasonally aboard boats provided by the Bureau of Commercial Fisheries Biological Laboratory at Galveston. The *R/V Redfish* was utilized for most stations, but the *R/V Skipjack* and a john boat were necessary for the shallow stations of East and West Bays.

Sampling was accomplished with the use of a 10–foot (3 m) otter trawl with 2-foot (61 cm) boards and a 10-fathom bridle. The trawl was made of webbing that was ¾-inch (2 cm) bar mesh or 1½-inch (4 cm) stretch. A cover formed from ¼-inch (6 mm) webbing was placed over the cod-end of the trawl to retain the smaller fish. The trawl was towed for 10 minutes at each station at about two knots. This speed and time allowed the coverage of about 20,000 square feet (1858 m^2) per trawl sample. The samples were placed in plastic cans and preserved with 10 % formalin.

The fish collected were separated to species, each species being individually counted and weighed to the nearest 0.01 gram. A species diversity index was calculated for species numbers and species weight for each catch using the Shannon-Weaver formula, $H' = -\Sigma\, p_i \log_e p_i$ natural bels/individual; where p_i is the proportion of the i^{th} species in the collection. H' is the diversity of the entire population, a value which cannot be determined for the fish population of an estuary. To apply this formula to a sample from a population, it must be estimated by, $H'' = -\sum \frac{N_i}{N} \log_e \frac{N_i}{N}$ natural bels/individual; where N_i is the number or weight of individuals in the i^{th} species and N is the total number or weight of individuals in the collection (Pielou 1966a). Because natural logarithms were used in the computations, diversity units are expressed as natural bels per individual (Pielou 1966b). Calculations, using diversity indices from several systems, indicate that diversity indices calculated with the H″ equation used for this study approximate normal distribution (Dr. N. E. Armstrong, personal communication). The use of statistics based on the normal distribution is thus justified.

As discussed by Wilhm and Dorris (1968), the diversity indices derived by the use of H″ are independent of sample size, a prerequisite when sampling fish populations. Another advantage of using H″ is that the addition or deletion of a species represented by only a few individuals does not change the diversity index to any great extent, especially when 6 or more species are already present. For example, the elimination of a species, represented by 5 fish, from the catch at Station 19 in February changed the resulting diversity indices from 0.923 to 0.095 for fish numbers and from 1.092 to 1.091 for fish weight.

To test the possibility that small changes in diversity were due to sampling as opposed to changes due to stress, ten duplicate trawls were taken during the study to obtain an estimation

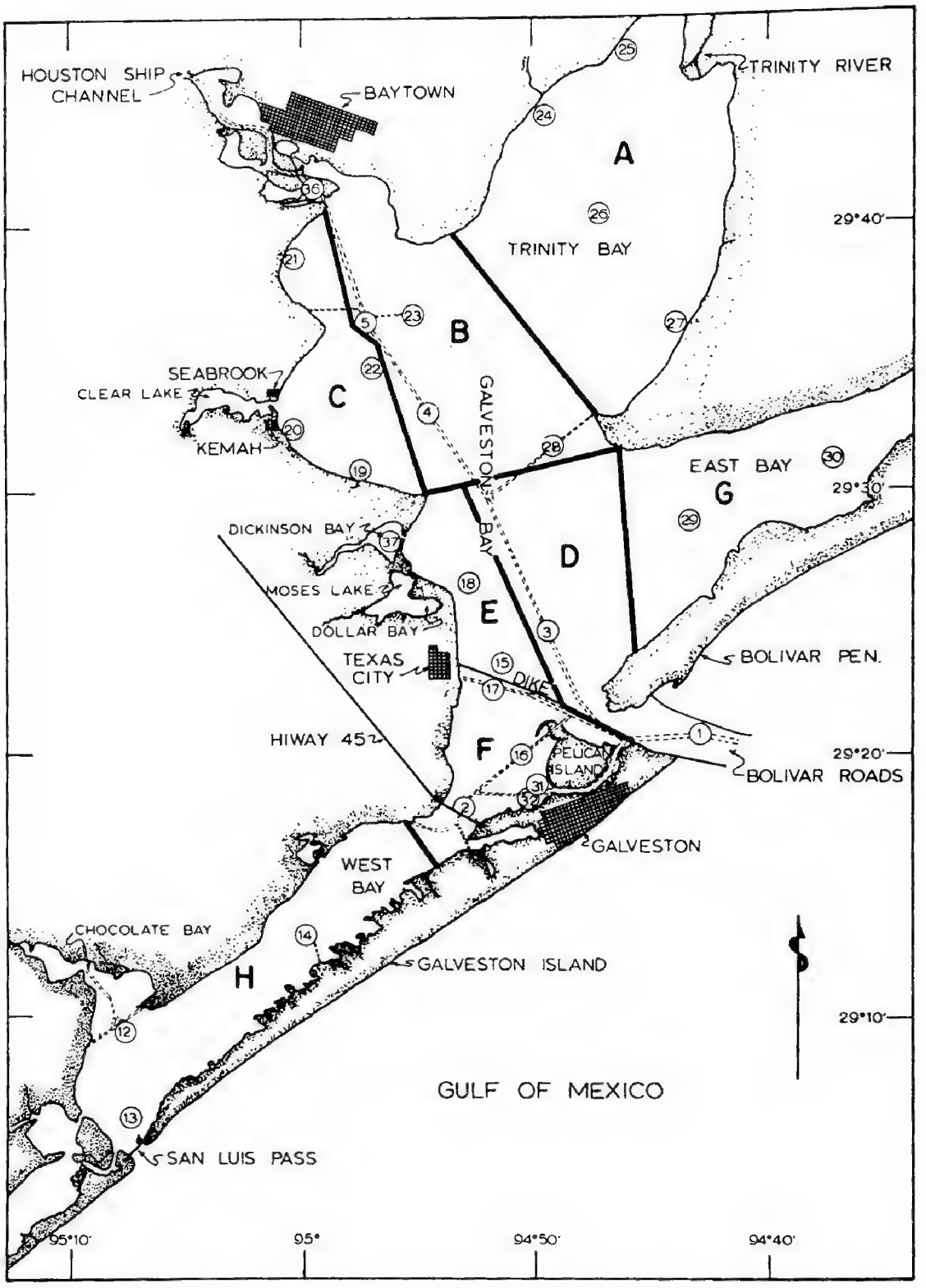

FIG. 1. Galveston Bay and Sampling Stations. Letters indicate ecological areas.

of trawling variation (Bechtel 1970). Results indicated very little trawling variability within stations, demonstrating that H″ is sensitive to changes in diversity due to stress.

A widely used method, with a wider scale for detecting changes due to stress, is the number of species/1000 individuals developed by Odum *et al.* (1960). Odum *et al.* (1963), Copeland (1966), Odum (1967) and Copeland and Cameron (1969) have shown that the number of species/1000 individuals is reduced in polluted waters, indicating that pollution causes stress. To quantify the relationship between diversity indices and the number of species/1000 individuals, a graph was made correlating the mean annual diversity computed for each station with the mean number of species/1000 individuals calculated for each station using the method of Odum *et al.* (1960) (Fig. 2). Because a linear relationship between the two measures of diversity is evident, both can be applied in environmental stress analyses. The number of species/1000 individuals is more easily understood, but is related to sample size.

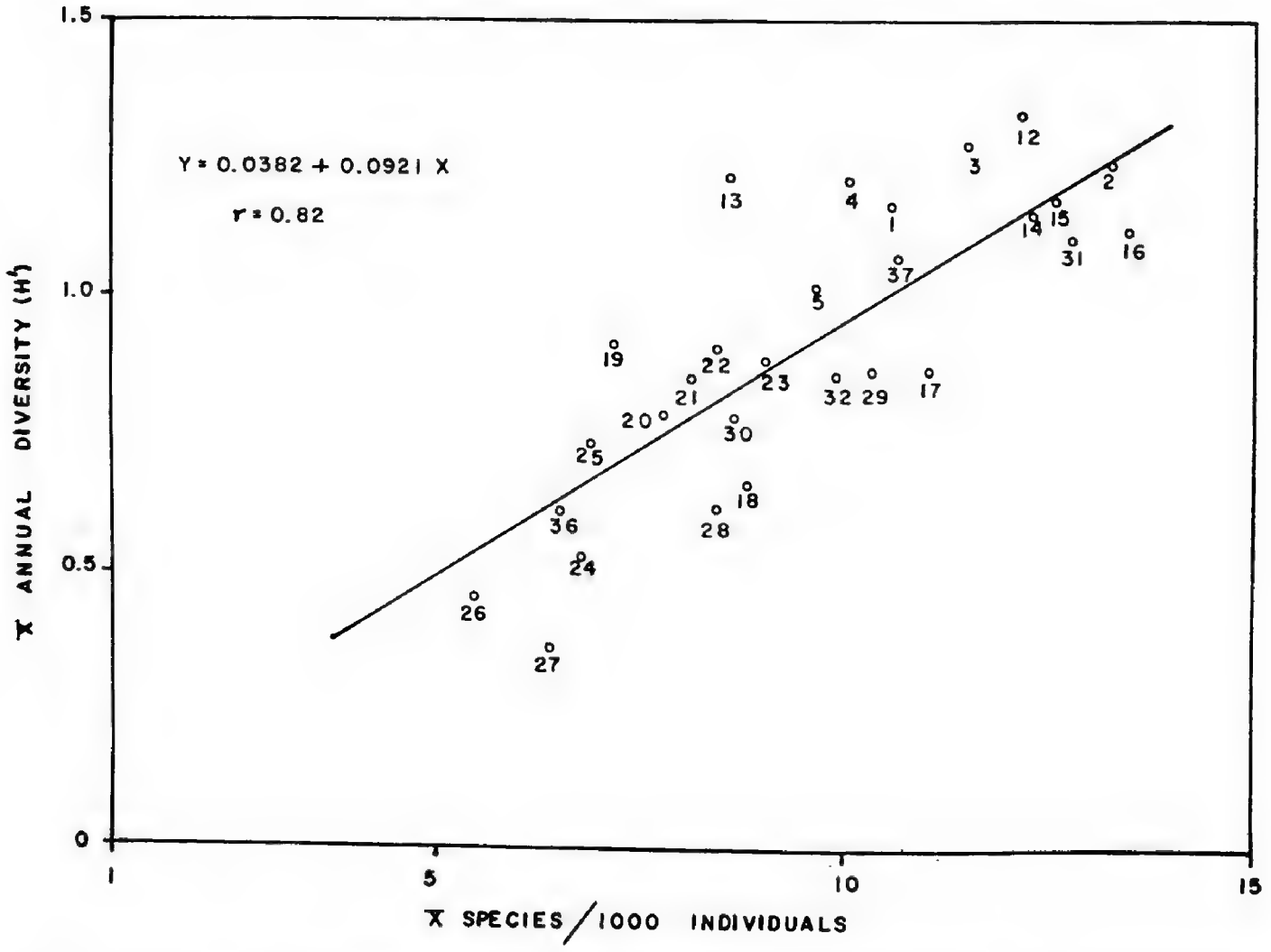

FIG. 2. Relationship between fish number diversity (natural bels/individual) and number of species/1000 individuals.

RESULTS

Environmental Parameters

The mean annual salinity encountered during the collection of organisms in February, April, July and October 1969, is plotted in Figure 3 using isohalines. The Galveston Bay system is essentially non-stratified except in the channels, where differences between the surface and bottom may be as large as 15 ppt. Examination of the isohalines indicates that a "tongue" of Gulf water runs up the main ship channel some considerable distance. A plume of fresh water apparently comes around the point near Station 28 and into East Bay.

The sites of major inputs of wastes into Galveston Bay are indicated in Figure 4. Most of the data were taken from a report by Gloyna and Malina (1964), which indicated the waste input volumes in 1963. In addition to these data, a more up-to-date volume (426 MGD) of waste entering via the Houston Ship Channel was provided by Reynolds and Eckenfelder (1970) through their "Reaction Rates" study. It is suspected that a considerable volume of waste enters via the Trinity River, but the volume or quality is unknown.

Trawling and Diversity Calculations

The fish collected during this study totaled 106,188 individuals, representing 66 species and weighing 206,783.79 grams. The February catch consisted of

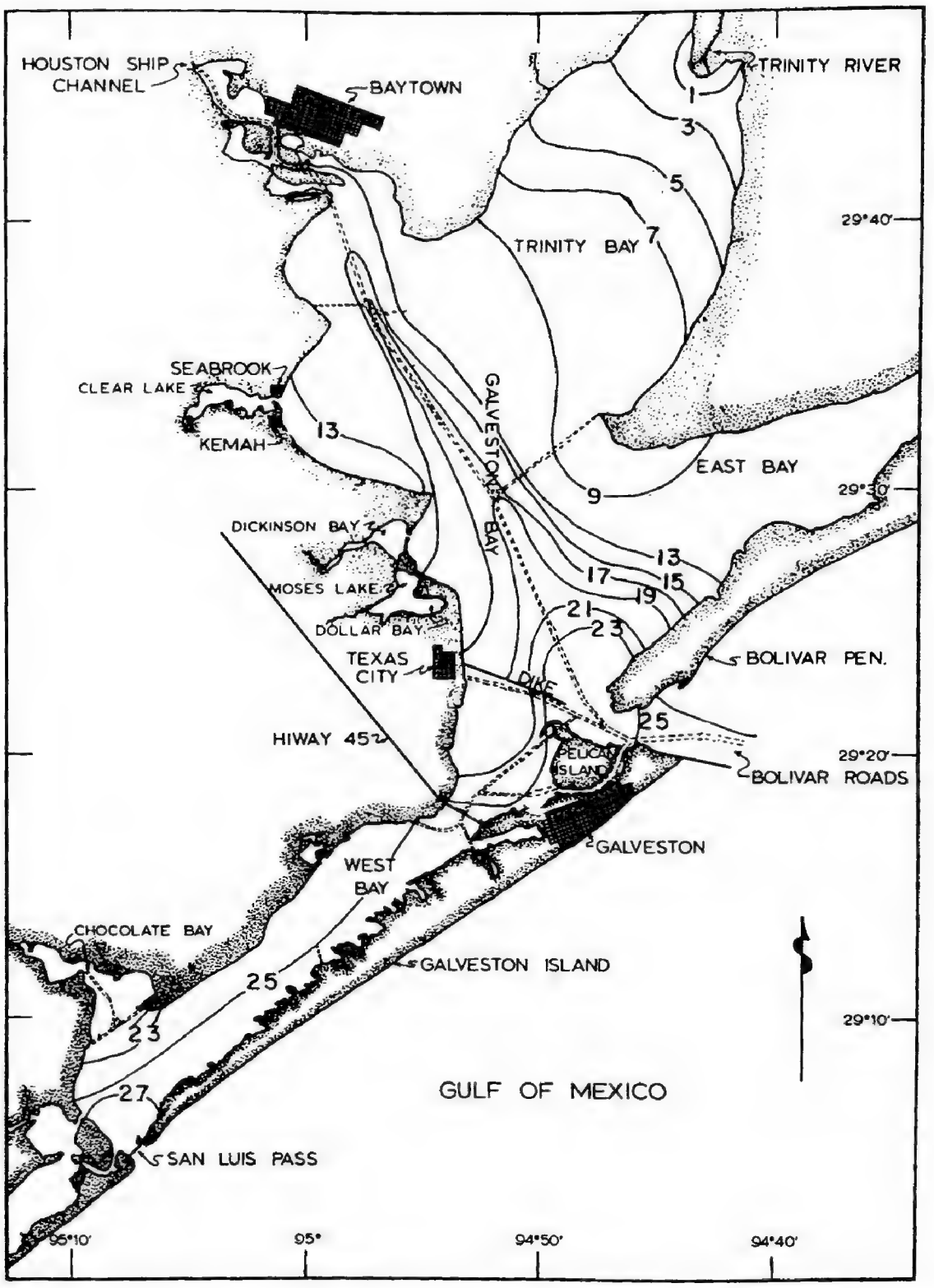

FIG. 3. Isohalines for the Galveston Bay system plotted from mean annual salinity (ppt) at each station. Data from collection cruises during February, April, July and October 1969.

26,242 individuals weighing 43,469.95 grams. Thirty-nine species were taken. The April catch showed a marked increase in both numbers of fish and total weight, with 41 species being caught. There were 49,705 individual fish which weighed 65,885.53 grams. The July catch consisted of 17,783 individuals, represented by 41 species, weighing 68,235.33 grams. The number of fish was considerably less than the previous sampling periods, however, total biomass increased indicating that the summer population was composed of more larger fish than were the winter and spring populations. The October sample represented

the smallest catch of the year for both numbers of fish and total weight, 12,458 individuals and 29,192.98 grams, respectively. Forty-four species were represented in the catch.

Of the 66 different species caught during the study, nine species were represented by only one individual and nine species were represented by only two individuals. Therefore, 18 of 66 species or 27.3% were represented by a total of only 27 of the total individuals or 0.025%. On the other hand, two species were

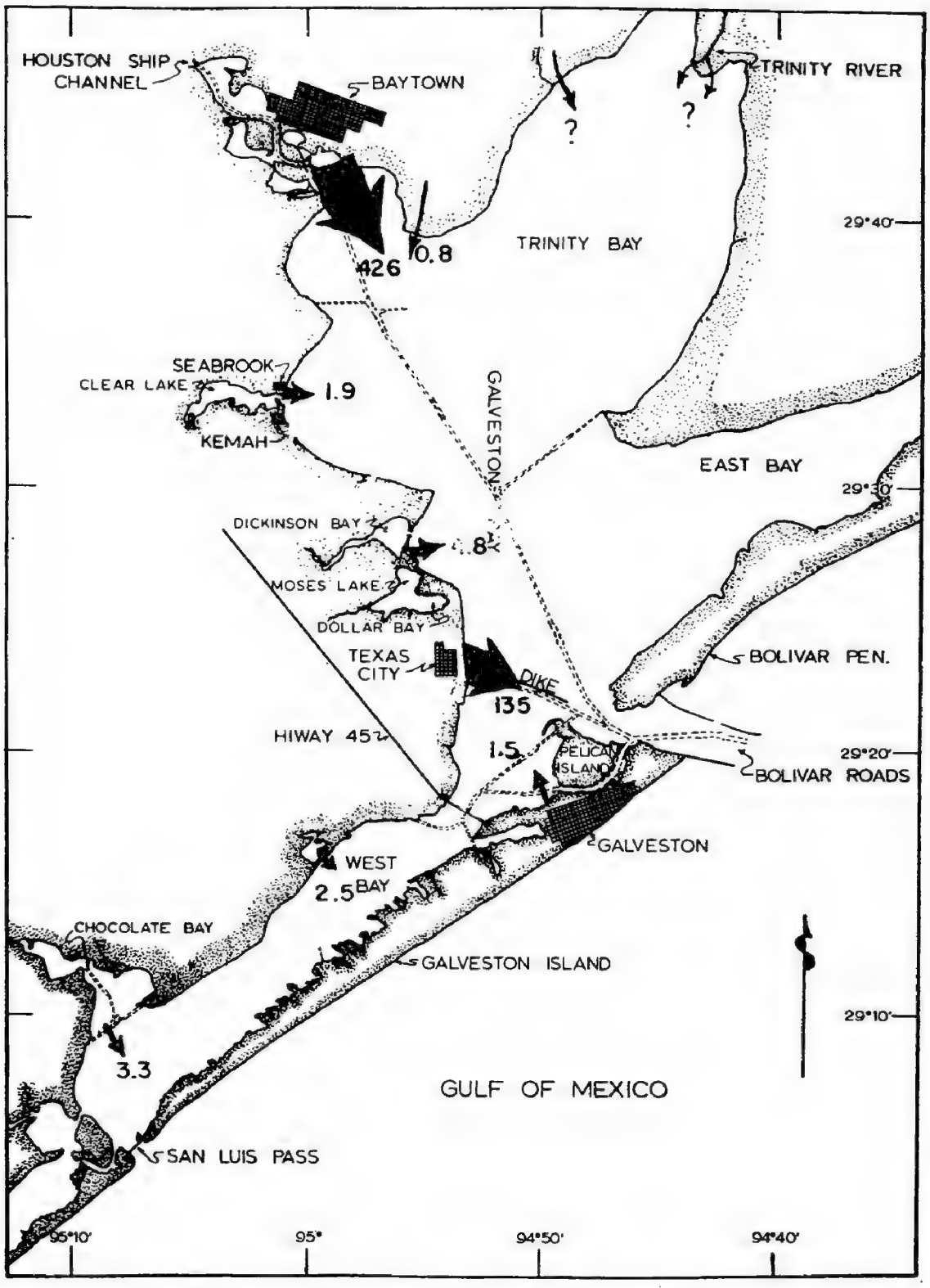

FIG. 4. Major waste input sites around Galveston Bay with approximate amounts of input in millions of gallons per day where known. Data from Gloyna and Malina (1964). Question marks indicate areas where wastes are thought to enter the bay, but the amount is not known.

TABLE 1

Dominant fish communities in Galveston Bay for each area during the four seasons

Area	Month	Most Abundant	Second Most Abundant	Third Most Abundant
A	Feb.	*Anchoa mitchilli*	*Micropogon undulatus*	*Brevoortia patronus*
	Apr.	*Micropogon undulatus*	*Anchoa mitchilli*	*Brevoortia patronus*
	July	*Micropogon undulatus*	*Anchoa mitchilli*	*Cynoscion arenarius*
	Oct.	*Anchoa mitchilli*	*Micropogon undulatus*	*Galeichthys felis*
B	Feb.	*Micropogon undulatus*	*Anchoa mitchilli*	*Leiostomus xanthurus*
	Apr.	*Micropogon undulatus*	*Anchoa mitchilli*	*Brevoortia patronus*
	July	*Micropogon undulatus*	*Galeichthys felis*	*Anchoa mitchilli*
	Oct.	*Galeichthys felis*	*Anchoa mitchilli*	*Micropogon undulatus*
C	Feb.	*Anchoa mitchilli*	*Micropogon undulatus*	*Leiostomus xanthurus*
	Apr.	*Micropogon undulatus*	*Anchoa mitchilli*	*Brevoortia patronus*
	July	*Micropogon undulatus*	*Cynoscion arenarius*	*Polydactylus octonemus*
	Oct.	*Galeichthys felis*	*Anchoa mitchilli*	*Ophichthus gomesi*
D	Feb.	*Micropogon undulatus*	*Menticirrhus americanus*	*Symphurus plagiusa*
	Apr.	*Micropogon undulatus*	*Polydactylus octonemus*	*Anchoa mitchilli*
	July	*Galeichthys felis*	*Cynoscion arenarius*	*Micropogon undulatus*
	Oct.	*Galeichthys felis*	*Micropogon undulatus*	*Menticirrhus americanus*
E	Feb.	*Anchoa mitchilli*	*Micropogon undulatus*	*Archosargus probatocephalus*
	Apr.	*Micropogon undulatus*	*Anchoa mitchilli*	*Leiostomus xanthurus*
	July	*Polydactylus octonemus*	*Micropogon undulatus*	*Anchoa mitchilli*
	Oct.	*Galeichthys felis*	*Cynoscion arenarius*	*Anchoa mitchilli*
F	Feb.	*Micropogon undulatus*	*Symphurus plagiusa*	*Anchoa mitchilli*
	Apr.	*Micropogon undulatus*	*Symphurus plagiusa*	*Anchoa mitchilli*
	July	*Micropogon undulatus*	*Stellifer lanceolatus*	*Cynoscion arenarius*
	Oct.	*Symphurus plagiusa*	*Etropus crossotus*	*Anchoa mitchilli*
G	Feb.	*Micropogon undulatus*	*Anchoa mitchilli*	*Mugil cephalus*
	Apr.	*Micropogon undulatus*	*Anchoa mitchilli*	*Leiostomus xanthurus*
	July	*Micropogon undulatus*	*Cynoscion arenarius*	*Galeichthys felis*
	Oct.	*Galeichthys felis*	*Anchoa mitchilli*	*Micropogon undulatus*
H	Feb.	*Micropogon undulatus*	*Anchoa mitchilli*	*Dasyatis americana*
	Apr.	*Micropogon undulatus*	*Leiostomus xanthurus*	*Anchoa mitchilli*
	July	*Micropogon undulatus*	*Leiostomus xanthurus*	*Cynoscion arenarius*
	Oct.	*Anchoa mitchilli*	*Sphaeroides nephelus*	*Dasyatis sabina*

represented by 93,577 individuals of the total catch or 88% and 119,105.57 grams of the total biomass or 57.6%. This apparent imbalance in the species diversity of fish is not to be unexpected in a naturally stressed estuary such as Galveston Bay (Odum and Copeland 1969). Reid (1955) found that 11 species constituted 99% of his trawl catches from East Galveston Bay.

Although many species were found to be distributed throughout the bay system, areas were found in which certain species exhibited a greater abundance than in other parts of the bay. A ranking system by total numbers and biomass was used to ascertain what were the dominant fish in each of eight bay areas which form more or less separate entities within the system (Fig. 1). These areas,

although somewhat arbitrary, are based on magnitudes of pollution inputs and environmental characteristics including physical boundaries. Because the anchovy, *Anchoa mitchilli*, and croaker, *Micropogon undulatus*, composed such a large proportion of the total catch in most areas, it was necessary to use the three most abundant fish in describing the dominant members of the communities for differences between areas to become evident. The differences encountered are indicated in Table 1.

The diversity indices calculated from both numbers and weights are listed in Table 2. In cases where duplicate trawls were made at a station, the index calculated from the combined catches has been used rather than the mean of the two individual samples. The winter range of diversity was from 0.112 (Station 22) to 1.576 (Station 3) for species numbers, and 0.099 (Station 24) to 1.896 (Station 4) for species weights. The spring range was from 0.022 (Station 36) to 1.179 (Station 2) and 0.055 (Station 27) to 1.520 (Station 1) for fish numbers and

TABLE 2

Fish Species Diversity Indices (Natural Bels/Individual) For Each Station in Galveston Bay

Station	February		April		July		October	
	H'_n	H'_w	H'_n	H'_w	H'_n	H'_w	H'_n	H'_w
1	.832	.839	1.052	1.520	.843	.430	1.963	1.888
2	.727	1.142	1.179	1.143	1.417	1.849	1.668	1.646
3	1.576	.500	.860	1.730	1.068	1.021	1.603	1.547
4	1.540	1.896	.604	.484	1.342	.759	1.343	1.185
5	1.240	.842	1.110	1.000	.783	.991	.936	1.348
12	.814	.945	..	..	1.585	1.914	1.594	1.972
13	.850	.733	..	..	1.680	.913	1.147	.517
14	..	..	.961	.873	1.786	1.821	.723	1.254
15	.889	1.857	.523	1.211	1.686	1.304	1.644	1.727
16	.692	.945	.695	1.101	1.133	1.658	1.989	1.928
17	.658	1.274	.700	.880	.871	1.240	1.276	2.219
18	.340	.439	.366	.862	.186	1.623	1.778	1.715
19	.905	1.091	.499	.883	1.716	1.417	.581	1.487
20	.119	.723	.823	.633	.745	.784	1.495	1.864
21	.871	.414	.334	.257	1.673	1.453	.525	1.822
22	.112	.226	.756	.816	1.408	1.195	1.381	1.485
23	.883	1.580	.652	.593	1.468	1.452	.580	.659
24	.862	.099	.140	.485	1.023	1.295	.095	.941
25	.896	1.100	1.032	.785	.871	.656	.157	.777
26	.525	.845	.355	.103	.869	.971	.091	.995
27	.374	.580	.183	.055	.695	1.092	.221	1.480
28	.699	.726	.243	.067	1.493	1.352	.212	1.341
29	.263	1.167	.776	.770	1.799	1.500	.640	1.611
30	.566	.952	.469	1.119	1.252	.906	.872	1.074
31	.502	1.277	1.060	1.373	.833	1.470	2.018	1.947
32	.736	1.036	.614	.795	.272	1.369	1.835	2.000
36	.142	.641	.022	.210	1.260	1.034	1.280	.799
37	..	..	.750	.754	1.543	1.345	.934	2.060
Means	.716	.918	.645	.789	1.175	1.239	1.092	1.475

weights, respectively. Most stations, especially those in Upper Galveston Bay and Trinity Bay, had a greater diversity in the summer than in the two previous seasons. The summer range was from 0.186 (Station 18) to 1.799 (Station 29) for species numbers and 0.430 (Station 1) to 1.914 (Station 12) for species weights. Some of the October samples exhibited the greatest diversity of the entire year. The range was from 0.091 (Station 26) to 2.018 (Station 31) and from 0.517 (Station 13) to 2.219 (Station 17) for fish numbers and weights, respectively.

Pooled diversity indices for numbers and weights. were computed for the entire bay system based on the total trawl catch for each season. Indices were also calculated for each of the eight bay areas (Fig. 1) by considering each area as one sample (Table 3). More species are included in the pooled trawl collection than in any of the individual collections made in that area. An average index is higher than a pooled index only when there is one species in very great abundance. Relative to the other species in the area represented by only a few individuals, this abundance is magnified by pooling, yielding a lower diversity index for the area. However, pooled indices are probably more representative of an area because the relative abundance of each species actually present in the area is more closely approximated in a pooled collection than in each individual collection. To illus-

TABLE 3

Pooled Fish Species Diversity Indices (Natural Bels/Individual) by Bay Areas

Area		Feb.	Apr.	Jul.	Oct.
Whole Bay	Numbers	.893	.934	1.592	1.308
	Weights	1.959	1.295	1.874	2.705
A	Numbers	.542	.624	.911	.127
	Weights	.716	.459	1.076	1.396
B	Numbers	.796	.179	1.450	1.393
	Weights	1.234	.741	1.215	1.727
C	Numbers	.554	.854	1.596	1.322
	Weights	1.683	.784	1.454	2.187
D	Numbers	.394	.949	1.072	1.960
	Weights	1.383	1.699	1.469	1.901
E	Numbers	.867	.889	.863	1.867
	Weights	1.719	1.212	1.880	2.117
F	Numbers	.715	1.119	1.140	2.017
	Weights	1.286	1.391	2.171	2.416
G	Numbers	.783	.720	1.432	.769
	Weights	1.411	1.101	1.090	1.356
H	Numbers	.817	.961	1.784	1.552
	Weights	.947	.873	2.126	2.033

trate, the one individual spot, *Leiostomus xanthurus*, collected at Station 27 in April does not appear to be as rare in that collection (1 of 4 species, 312 individuals) as it actually was in all of Trinity Bay, for it was the only one present in the entire pooled trawl catch which consisted of 9 species and 4004 individuals. This one fish thus contributed more to average area diversity than its singular presence in the community warranted.

DISCUSSION

Life-History Effects on Diversity

One characteristic of an estuarine fish population is that many of the species are not permanent residents, but spend only part of their life cycle in the estuary. Migrations form an integral part of the life-history of many species. These migrations reoccur in yearly or seasonal cycles, many being for the purpose of spawning. Larval and postlarval fish immigrate into the estuary, use these highly productive nursery areas during early development, and then emigrate back to the sea as young adults. Because migrations and recent spawnings can affect the fish diversity of the estuarine population, knowledge of the life-history of the species involved is necessary for predictive purposes (Lloyd 1964). The species collected which showed evidence of recent migrations and/or spawning are indicated in Tables 4 and 5.

The seasonal pattern of variation of the fishes in the Galveston Bay estuary is such that the fall population is the smallest in both numbers and biomass. For the species that spawn in the Gulf, this is the period when most mature adults are

TABLE 4

Species Displaying Distinct Migration Patterns During Study

Species	First Caught in Bay	Last Caught in Bay
Elops saurus	April	April
Synodus foetens	April	October
Myrophis punctatus	April	October
Urophycis floridanus	February	April
Caranx hippos	July	July
Chloroscombrus chrysurus	July	October
Selene vomer	July	July
Vomer setapinnis	July	July
Orthopristis chrysopterus	April	October
Menticirrhus americanus	February	October
Micropogon undulatus	February	October
Stellifer lanceolatus	April	October
Rissola marginata	April	April
Polydactylus octonemus	April	October
Citharichthys spilopterus	February	October
Etropus crossotus	February	October
Symphurus plagiusa	February	October

TABLE 5

Species Showing Indication of Spawning During Study

Species	Probable Spawning Period	Location of Spawning
Elops saurus	Late Feb.–April	Gulf
Brevoortia patronus	Late Oct.–April	Gulf & Bay
Anchoa mitchilli	Extended	Gulf & Bay
Synodus foetens	Late Winter–April	Gulf
Galeichthys felis	June–July	Bay
Myrophis punctatus	Nov.–March	Gulf
Chloroscombrus chrysurus	May–Sept.	Gulf
Cynoscion arenarius	April–Oct.	Bay
Leiostomus xanthurus	Nov.–March	Gulf
Menticirrhus americanus	April–Oct.	Gulf
Micropogon undulatus	Oct.–Feb.	Gulf
Stellifer lanceolatus	April–Oct.	Gulf
Chaetodipterus faber	April–Oct.	Gulf
Prionotus tribulus	Sept.–Late Winter	Gulf
Gobionellus boleosoma	Extended	Gulf & Bay
Citharichthys spilopterus	Late Winter–April	Gulf
Etropus crossotus	Summer	Gulf
Symphurus plagiusa	April–Oct.	Gulf
Sphaeroides nephelus	Late Winter–April	Gulf

absent from the bays. The newly spawned fish begin migrating into the bays from late fall throughout the winter and early spring. The numbers and biomass of fish in the bays increase correspondingly. The number of fish present is at a maximum in the spring. The mortality rate is high, causing a sharp decrease in numbers throughout the summer. However, the surviving fish grow rapidly so that the summer population has the greatest biomass. Chin (1961) found that the croaker, southern flounder, menhaden and spot increased in numbers in Clear Lake until May and then decreased. The sand trout, sea catfish, gafftopsail catfish, and bay whiff reached their peak in the summer and then declined. Except for the two species of catfish and the bay whiff, the same patterns were observed during this study.

There are two migration patterns which are evident. The spawning migrations of adults out of the bays and those of postlarvae and juveniles into the bays have the greatest effect on the species diversity since thousands of individuals are involved.

Migrations of species in response to seasonal temperature changes were noticed. Those species which showed a migration out of the bay with increasing temperature were the hake and the tonguefish. A great many more species entered the bay as the temperature increased, but the total number of species caught during each season was rather constant.

Several low diversity indices obtained at stations normally exhibiting a medium to high diversity were the result of life-history phenomena. It is necessary to separate these low indices from those which are the result of environmental and pollutional stress.

Both the number and weight indices at Station 1 in February were low, despite the presence of 16 species, due to the great number of postlarval *Micropogon undulatus* captured as they migrated into the bay. Station 15 showed a decrease in both indices due to a large increase in the *Anchoa mitchilli* population in April. The appearance at Station 5 in July of a large number of star drum, *Stellifer lanceolatus*, resulted in a lower number index, but had very little effect on the weight index due to the small size of the fish. Similarly, an increase of the *Anchoa mitchilli* population at Station 32 in July caused a decrease in the number index with no effect on the weight index.

The decreases noted in the number indices at many of the stations in Upper Galveston Bay between July and October were due to a decrease in the number of species present, but more important to an increase in the number of *Anchoa mitchilli*. In East Bay, the increase of this species was in itself the cause for the decrease in number diversity as the number of species increased from 8 to 10. The same situation was apparent in Dickinson Bay, where, despite a gain of four species between July and October, the number index was substantially lowered because of an increase of *Anchoa mitchilli*.

These patterns of increase in abundance of one species are also apparent from examination of Table 1. One species may substantially lower the diversity of an area below its yearly average for a short period of time. To illustrate, the low diversity at Station 37 in April was chiefly due to the large numbers of *Micropogon undulatus*, but in October *Anchoa mitchilli* was the abundant species. Careful analysis must be made to ascertain if these differences are due to life-history phenomena or to actual water quality degradation.

Since nearly all areas of the bay are affected in one season or another by migratory patterns, it appeared necessary to eliminate the seasonal variation by averaging the diversity indices of each station and bay area. Thus, for an annual analysis of the effects of stress on diversity, mean annual diversity indices should be utilized.

Analysis of Differences Between Number and Weight Indices

Wilhm (1968) stated that diversity indices computed on weights of organisms gave a more realistic index than did indices computed on numbers, because biomass units were more closely associated with ecological energetics than were numbers of organisms. However, the number of individuals present in a community represents the number of energy pathways available for energy transfer (MacArthur 1955; Armstrong *et al.* 1968).

For these reasons both a number and a biomass index were computed for each trawl collection. The resulting indices were compared using Student's t test to determine if any significant differences existed between the two sets of indices for each sampling period (Table 6). Average weight indices were greater than average number indices in all seasons. Three of the four seasons showed a significant difference at the 95% confidence level. There was no significant difference between the July indices. Analysis of the trawl catches by both numbers and

weights appeared justified because different conclusions concerning the effects of stress might be drawn if each index was applied separately, especially since the annual difference was highly significant.

Assuming that weight indices are more realistic than number indices, stations with a weight index substantially lower than its corresponding number index were examined to ascertain the cause.

Station 13 consistently had a greater number index than weight index and was the only station to exhibit this pattern. This area is able to support a more diverse population of numbers of fish than biomass. This is apparently due to the fact that, except for two channels, water depth varies between a few inches and two feet. The bottom is constantly shifting under the influence of tidal currents through San Luis Pass which allows for less habitat diversity.

At Station 3 in February, 34 *Menticirrhus americanus* accounted for 89% of the weight creating a much less diverse community in terms of biomass. Similarly, two sheepshead, *Archosargus probatocephalus*, captured at Station 21 in February, accounted for 89.7% of the biomass. A substantial increase in the *Polydactylus octonemus* population at Station 15 in July was rseponsible for the lower weight index, although an overall weight diversity increase occurred between April and July.

The large differences encountered at the Upper Galveston Bay and East Bay stations in April and July were due to the great abundance of juvenile croaker, *Micropogon undulatus*, relative to the other species present. This decrease in weight diversity in the spring and summer can be expected to reoccur each year and will be most noticeable in areas which do not support a large number of species.

It thus appears that if the seasonal occurrence of recently spawned individuals is taken into consideration in areas having few species and, if one or two exceptionally large individuals are excluded from catches in which the majority of fish are small, the weight index will normally be larger than the number index.

For diversity studies of organisms composing the higher trophic levels of a community, it is desirable to calculate indices based on both numbers and weights of individuals. Because one species may dominate a community at certain times of its life cycle, indices which take this into account as well as those which tend

TABLE 6

Comparison of Number and Weight Diversity Indices (Natural Bels/Individual) For Each Season

February:	Number vs Weight	t = 2.150*	(2.060)
April:	Number vs Weight	t = 2.338*	(2.060)
July:	Number vs Weight	t = 0.697	(2.052)
October:	Number vs Weight	t = 3.695**	(2.771)
All Seasons:	Number vs Weight	t = 4.351**	(2.660)

* Significant at 95% confidence level.

** Significant at 99% confidence level.

Numbers in parentheses are tabular t values.

to de-emphasize this influence should be used to adequately assess the species' influence on the diversity of the community.

Comparison of Galveston Bay Diversity With Other Texas Coast Bays

Three factors influence the diversity index of a fish catch; *i.e.*, the number of individuals, the number of species and the distribution of the individuals among the species. Variation in any one of these can change the resulting diversity index.

Sager and Hasler (1969) found considerable variation in the indices of diversity calculated for phytoplankton samples from three Wisconsin lakes. The number of species ranged from 14 to 39. By plotting the number of species in a sample against the diversity index for the sample, they concluded that the number of species made only a minor contribution to the diversity variation. A similar plot was made using the mean annual number of species encountered at each station against the mean annual diversity (Fig. 5). A direct relationship can be observed. The differences between the phytoplankton data and this fish data may be attributed to the fact that the number of species of fish is considerably fewer, but is more probably due to differences in the systems from which the samples were taken. The phytoplankton were from three freshwater lakes and the fish were from a multiple-stressed estuary. The direct relationship observed in Galveston Bay indicates that those areas with the smallest species composition also have the lowest mean annual diversity.

Stress tends to eliminate the more sensitive species from a system, reduces competition and allows for a greater abundance of the more resistant species. A greater amount of unevenness results. More species may be required to compose a community of given diversity in a stressed system than would be necessary to obtain the same diversity in a system not experiencing the same stress or receiving less stress.

Predictive equations for determining species diversity from the number of species in a sample were obtained for both fish weights and numbers by regression analysis. These equations are:

$$H'_n = -0.0736 + 0.1062\ S, \text{ and}$$
$$H'_w = -0.0132 + 0.1237\ S;$$

where H'_n and H'_w are the diversity indices for fish numbers and weights, respectively, and S is the number of species in the sample. Theoretically H′ should equal zero when S equals one.

These equations were applied to trawl catch data of Hoese *et al.* (1968) from Aransas Bay, Texas. This bay is similar to Galveston Bay except that it is considered not to be polluted. Four sets of trawl data, one from each of the same seasons sampled during this study, were selected for computation of diversity indices. The results (Table 7) indicate that the Aransas Bay fish number diversity was greater than expected, based on Galveston Bay's predictive equation, during summer and fall. Aransas Bay fish weight diversity was also greater than expected during the winter and fall.

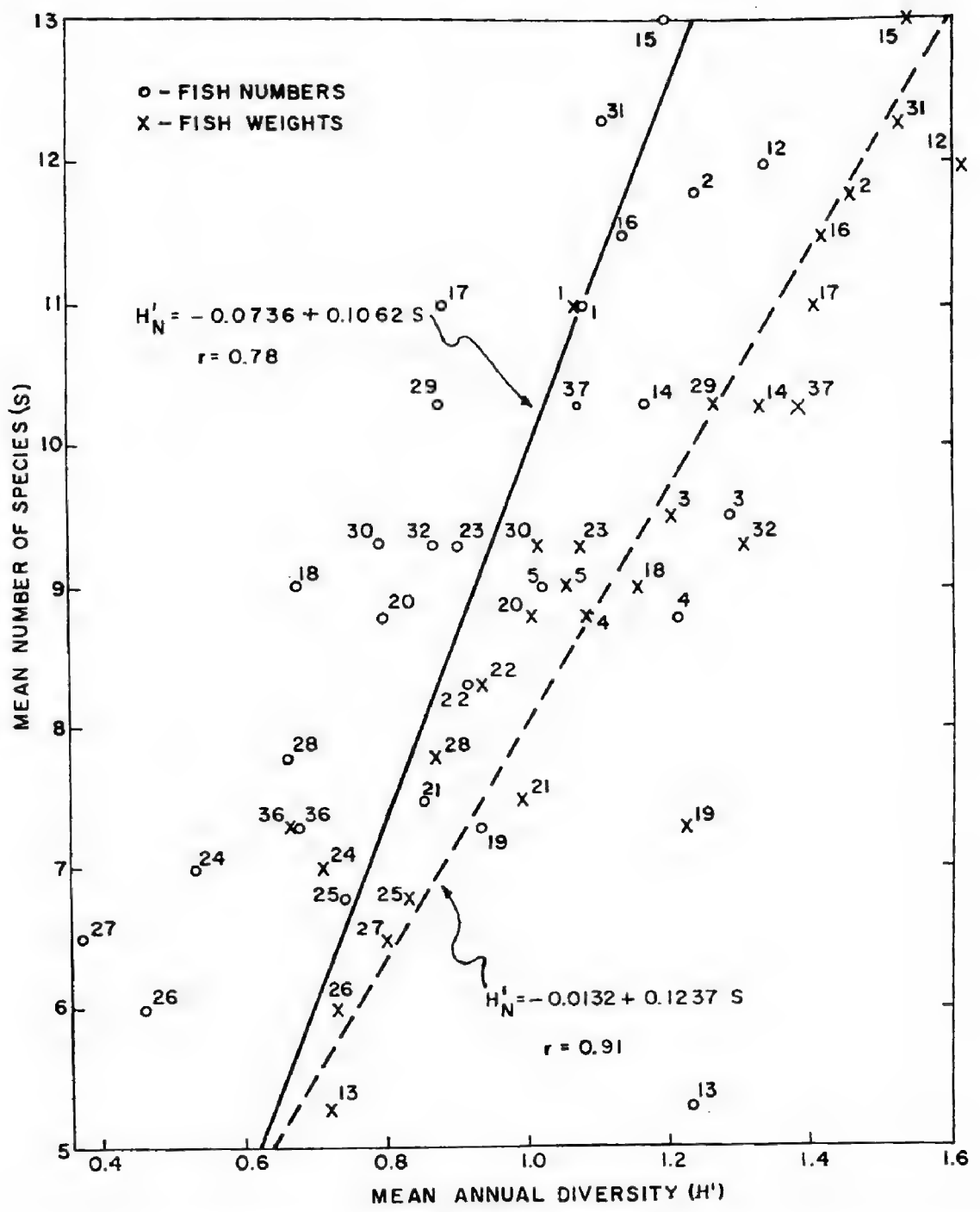

FIG. 5. Relationship between number of fish species and diversity (natural bels/individual) for all Galveston Bay stations.

The predictive equations were also applied to unpublished data of a University of Texas Marine Science Institute Estuarine Ecology class that made trawl hauls in Aransas, Redfish and Corpus Christi Bays on 21 June 1968. The results indicate that Aransas Bay and Redfish Bay had greater diversities than were expected, while Corpus Christi Bay had lower diversities than expected. The station sampled in Corpus Christi Bay was in the vicinity of an aluminum plant's effluent discharge point.

In general, then, the other bays have a greater fish number and fish weight species diversity than does Galveston Bay.

The mean annual diversity of Aransas Bay for 1965 was 1.430 for fish numbers and 1.888 for fish weights. Both these values were greater than would be expected in Galveston Bay, 1.360 and 1.657, respectively, based on 13.5 species.

TABLE 7

Comparison of Galveston Bay Diversity (Natural Bels/Individual) With That Expected For Other Texas Coast Bays

Bay	Date Sampled	No. of Species	Exp. H'_n	Calc. H'_n	Exp. H'_w	Calc. H'_w
Aransas	2-15-65	14	1.413	1.234	1.719	1.897
	4-29-65	16	1.626	1.482	1.966	1.970
	8-18-65	16	1.626	2.089	1.966	1.824
	10-20-64	8	.776	.916	.976	1.859
	6-21-68	11	1.095	1.266	1.348	1.505
Corpus Christi	6-21-68	17	1.732	1.515	2.090	1.414
Redfish	6-21-68	9	.882	1.334	1.100	1.756

These few calculations indicate that, due to pollution, the diversity of the fish populations of Galveston Bay are lower than other similar coastal bays.

Relative abundance data for Galveston Bay fishes are available from several studies (Reid 1955, 1956, 1957; Chambers and Sparks 1959; Chin 1961). Of the 11 most abundant fish listed by Reid (1955), 9 were found to be among the 13 most abundant in this study. Reid, however, worked strictly in East Bay during the summer only and used three different types of fishing gear, thereby capturing more pinfish and mullet than were taken in this study. Diversity indices based on fish numbers were calculated for some of the summer trawl collections listed by Reid (1956, 1957). A comparison with the number index obtained during this study for Stations 29 and 30 in July is made in Table 8. Because the majority of the fish species and their relative abundances were similar to those taken during Reid's studies, the small differences in diversity indicate that the trawl variation must be rather constant.

TABLE 8

Diversity Indices (Natural Bels/Individual) for East Bay Calculated from the Sources Indicated

Fish Number Diversity Index	Source
1.335	Reid (1956), Table 5 (Based on total catch—35 species—of 78 trawls made in summer of 1955).
1.210	Reid (1957), Table 2 (Based on 11 most abundant species taken in 78 trawl hauls made in summer of 1955).
1.206	Reid (1957), Table 3 (Based on 9 most abundant species taken in 16 ten-foot otter trawl hauls made in summer of 1954).
1.119	Reid (1957), Table 3 (Based on 8 most abundant species taken in 40 ten-foot otter trawl hauls made in summer of 1955).
1.430	Reid (1957), Table 3 (Based on 8 most abundant species taken in 34 ten-foot otter trawl hauls made in summer of 1956).
1.432	This Study, Table 3 (Based on 12 species taken in 3 10-foot otter trawl hauls made in July 1969).

TABLE 9

Significance of Differences in Diversity (Natural Bels/Individual) Between Seasons as Determined by Student's t Test

	Fish Numbers		
	April	July	October
February	0.880 (2.069)	4.113** (2.787)	2.620* (2.060)
April	..	4.750** (2.787)	3.625** (2.787)
July	..	..	0.679 (2.052)
	Fish Weights		
	April	July	October
February	1.173 (2.069)	2.647* (2.060)	4.165** (2.787)
April	..	3.576** (2.787)	7.125** (2.787)
July	..	..	2.256* (2.052)

* Denotes significance at 95 % confidence.
** Denotes significance at 99% confidence.
Numbers in parentheses are tabular t values.

Analysis of Variance

The existence of seasonal differences in diversity for the entire bay system was indicated from a comparison of average diversity indices (Table 2). To determine if any of the seasonal differences encountered were significant, Student's t test were employed to compare paired station indices for all possible combinations of seasons taken two at a time (Table 9).

There were no significant differences for fish numbers or weights between February and April. The February and April indices for both numbers and weights were significantly different from those of July and October. The July fish number indices were not significantly different from those of October; however, the weight indices were significantly different at the 95% confidence level.

There is thus a real seasonal change in diversity in Galveston Bay when the system is considered as an entity. The winter and spring seasons exhibit the lowest diversity with an increase occurring into the fall.

To determine what areas (Fig. 1) were significantly different from each other in diversity within a single sampling period, Duncan's Multiple Range Test was applied to both the average number and average weight indices.

The differences encountered between the areas in February were not significant for fish numbers or fish weights. The expected salinity gradient was not present in February and above average salinities were evident throughout Upper Galveston Bay and Trinity Bay. This was apparently caused by high tides, eight to nine feet above normal, which occurred during the night of 13 February 1969. A rather thorough mixing of lower bay and Gulf water with the upper bay water resulted, making conditions relatively uniform throughout the system and upsetting whatever sharp diversity differences that may have been present.

In April, West Bay (Area H) had a significantly greater fish number diversity than did Trinity Bay (Area A), but differences between other areas were not significant. More differences are significant, however, when fish weight diversity

indices are compared. Areas A and B in Upper Galveston Bay were significantly lower ($p = 0.05$) in diversity than all the other areas. Area C was only lower than Area D, while Area D was higher than all of the other areas. At the 99% confidence level, Areas B and C were significantly different from Area D, while Area A was significantly lower than Areas F and D.

In April, then, Upper Galveston Bay had a significantly lower diversity than did the lower portions of the estuary. There were no differences within these two larger areas except that the lower portion of the Houston Ship Channel (Area D) had a greater diversity than did its surrounding areas.

The July comparisons indicate that, based on fish numbers, West Bay (Area H) had a greater diversity ($p = 0.05$) than did Trinity Bay and Area F with no other area differences being significant. The fish weight diversity in Area D was significantly lower ($p = 0.05$) than the other sections of Lower Galveston Bay and West Bay. Trinity Bay had a significantly lower diversity ($p = 0.05$) than did West Bay and the Texas City-Galveston region (Area F).

Differences encountered in October were of greater significance than in the previous seasons. Area F was higher ($p = 0.05$) in fish number diversity than Upper Galveston Bay and East Bay (Area G). Except for Area C, these differences were also significant at the 99% confidence level. Trinity Bay was significantly lower than all other areas except East Bay at 95% confidence and lower than all other areas, with the exception of East Bay and Area B, at 99% confidence. Based on fish weights, Areas A and B were lower ($p = 0.05$) than all other areas of the bay except East Bay and West Bay. Area H had a lower diversity ($p = 0.05$) than Area F. At 99% confidence, Areas A and B were only significantly different from Areas E and F.

In general, then, the upper portions of the Galveston Bay system support fish populations which are significantly lower in diversity than West Bay and those areas around Galveston Island and Texas City. These differences in diversity were maintained from April through October, but were not significant in February. The relative position of some of the areas changes between seasons and also when weights and numbers are compared within a given season, but the overall indication is that the lower portion of the estuary is significantly greater in diversity.

A comparison of the mean annual diversity indices for both numbers and weights of fish at each station with the means of every other station was desired to determine which stations were significantly different from each other for the entire year. The use of means eliminates seasonal fluctuations and compares the average conditions encountered.

Any station which had a significantly reduced diversity for the entire year could be considered to be severely stressed on a continuous basis. Duncan's Multiple Range Test was employed for this determination. The results indicated that Stations 2, 3, 12, 15 and 31 had significantly greater diversity than Stations 24, 27 and 36. Because Station 13, considered to be severely stressed naturally, was not significantly different from those stations having a high annual diversity, the significant differences encountered are apparently due to a combination of environmental and pollutional stresses. Parts of Trinity Bay and the Houston Ship-

Channel north of Morgan Point are unable to support a diverse fish community on an annual basis, although at certain times conditions may permit diverse populations to occur in these areas. The moderately high indices which were obtained at Station 36 in July and October and at Station 24 in July are evidence of fluctuating conditions.

Relationship Between Diversity and Sources of Pollution

The Galveston Bay estuary has been classified as an emerging new system associated with man (Odum and Copeland 1969) and is considered to be a multiple-stressed system. A multiple stress is defined in this classification system as the combined effect of many different types of materials causing stress in varying degrees, and in fluctuating amounts. A major characteristic of such a system is the patchiness which results from concentrated drifting wastes.

Galveston Bay receives a conglomerate of domestic sewage, industrial effluents (predominently petrochemical wastes) and seafood processing wastes (Fig. 4). The stress exerted by these materials is in addition to those caused by the normal environmental fluctuations of temperature, salinity and dissolved oxygen. Some of the effluents are received directly from cities and industries located around the periphery of the bay. Wastes are also transported into the estuary via the Trinity and San Jacinto Rivers, the Houston Ship Channel and the numerous small bayous bordering the bay. The major source of industrial wastes is from the many industries located along the Houston Ship Channel between Baytown, Texas and the City of Houston. It is estimated that the amount of industrial effluent discharged into the channel averages about 426,000,000 gallons per day (Reynolds and Eckenfelder 1970). The Trinity River's contribution of municipal and industrial wastes from the cities located along its banks is estimated to be large, but is not known. No recent data as to total amounts of domestic and industrial wastes discharged into the bay system are available, but Gloyna and Malina (1964, Table H-1) present a summary of data collected up to that time. The amounts reported have probably increased substantially as the Houston Ship Channel was estimated to be receiving only 167,234,100 gallons of effluent per day.

A principal established during previous pollution studies is that as distance from a source of pollution or stress increases there is a corresponding increase in species diversity. The correlation between source and distance has been shown to exist for zooplankton (Odum *et al.* 1963; Copeland 1966; Copeland and Wohlschlag 1968), phytoplankton (Patten 1962), benthic macroinvertebrates (Wilhm and Dorris 1966; Storrs *et al.* 1969) and fish (Tsai 1968; Armstrong *et al.* 1970). This relationship may also be observed in Galveston Bay. The average diversity at Station 19 is greater than that at Station 20 for both fish weights and numbers despite the fact that Station 20 had an annual average of 1.5 more species. Several large seafood processing plants are located along the channel leading into Clear Lake. Odum *et al.* (1963) showed that areas receiving wastes from seafood packing plants were high in total phosphorus and had a lowered zooplankton diversity. The mean annual nutrient data indicate that Station 20 had a higher phosphorus

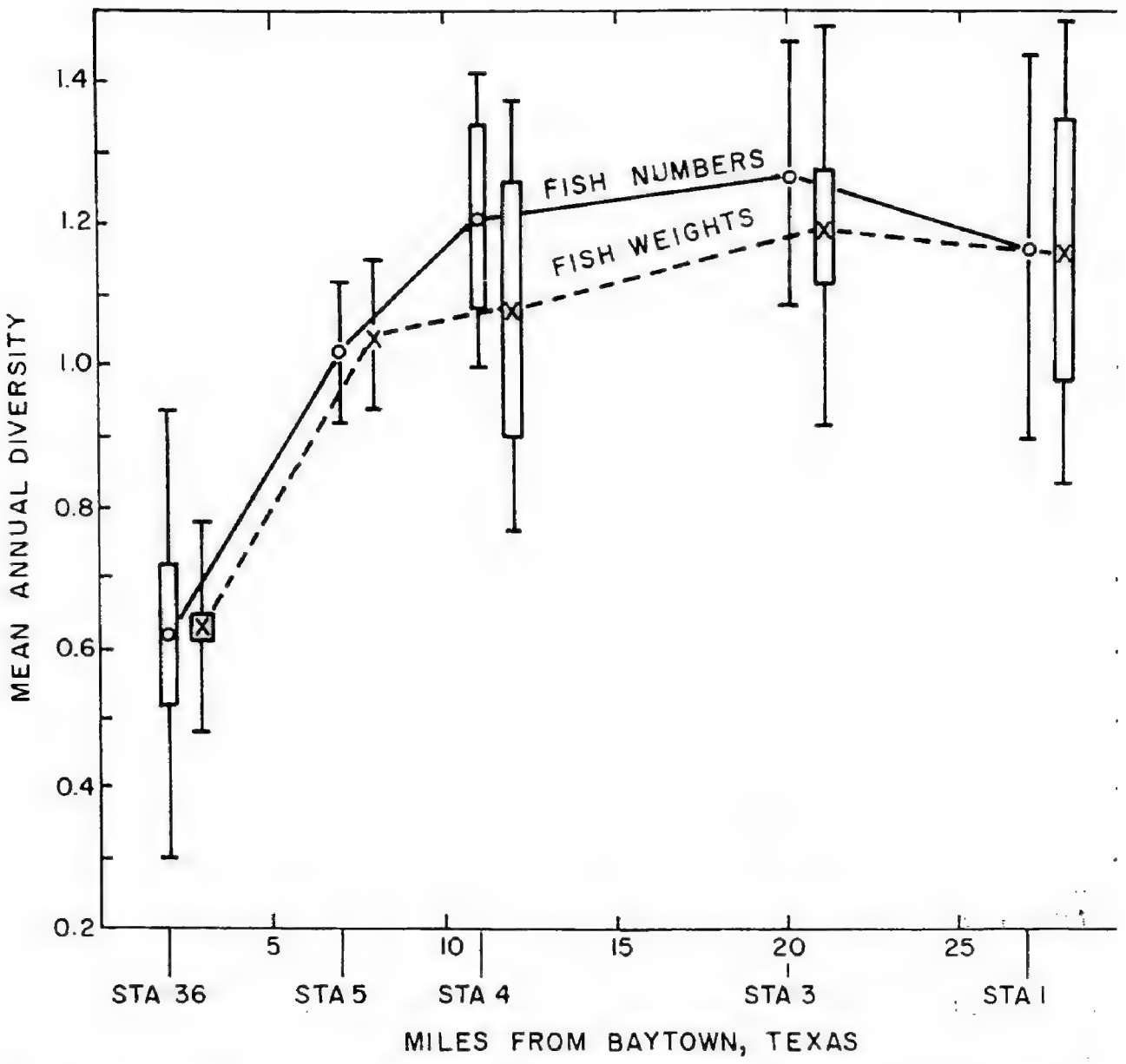

FIG. 6. Relationship between diversity (natural bels/individual) and distance in the Houston Ship Channel. Vertical lines represent ± 1 standard error of the mean. Vertical bars represent ± 1 standard error of the mean attributed to environmental influence.

and nitrogen concentration, 1.237 mg/l and 1.358 mg/l, respectively, than did Station 19, 0.783 mg/l and 0.918 mg/l, respectively. The water entering the bay through the Clear Lake channel is thus a source of pollution in the immediate area of Seabrook and Kemah.

Estimates of the variation of averaged diversity indices attributable to trawling have been made. The total amount of variation of the means, as indicated by standard errors, is represented at each station in Figures 6 and 7 by vertical lines. The amount of variation due to environmental influences is represented by vertical bars. The differences encountered between stations are more evident with the variation due to trawling separated in this manner. In addition, averaging the diversity indices eliminates the seasonal variations due to life-history phenomena. The means thus represent average conditions and can more easily be compared with average environmental characteristics.

A change in diversity occurs as distance down the Houston Ship Channel increases (Fig. 6). Conditions improve consistently, as evidenced by the increase in diversity, from Station 36 until Station 3 is reached. The decrease between

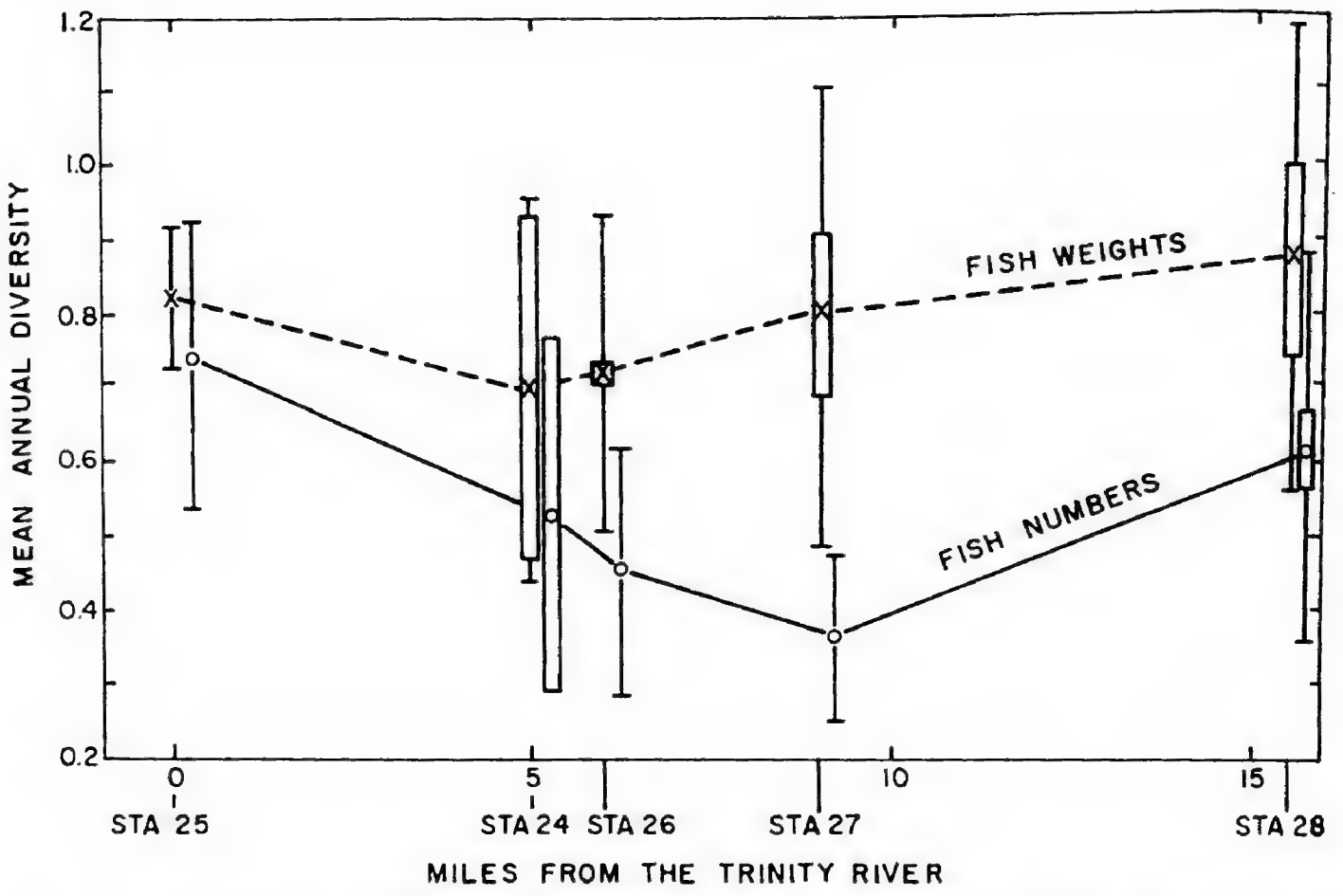

FIG. 7. Relationship between diversity (natural bels/individual) and distance in Trinity Bay. Vertical lines represent ± 1 standard error of the mean. Vertical bars represent ± 1 standard error of the mean attributed to environmental influence.

Stations 3 and 1 is due to the natural environmental stress associated with the fluctuating tides and currents encountered at Bolivar Roads and not to pollution stress. The depth of these Houston Ship Channel stations causes considerable stratification in the water column. The higher salinities occurring in the channel are due to a salt water wedge which extends up to Morgan Point (Fig. 3). It is believed that the channel should be considered separately from the rest of the bay because it acts as a "river" flowing down the length of the estuary. The dilution of the effluents entering the system above Morgan Point can be directly equated with distance from the source. In addition to depressed species diversity at Station 36, other deleterious effects of the toxic effluents passing through the area were noticed. Many of the fish captured in this area were in poor physical condition. A great many were missing caudal fins and some were also missing filamentous portions of pectoral and pelvic fins. This condition is due to the corrosive action of non-biodegradable substances in the water (D. E. Wohlschlag, personal communication). Others had the eyes covered with a hard, white crust and it was assumed that these fish were blind.

The fate of the petrochemical effluents being dumped into the ship channel above Morgan Point was investigated by Calder and Parker (1968) with the use of $^{13}C/^{12}C$ isotope ratios of dissolved and particulate organic matter. They obtained values above Baytown, Texas ranging from −26 to −48.8; a range of −16 to −21 was considered to be normal for an unpolluted system. They conducted limited sampling in Galveston Bay and obtained values from two upper bay areas

of −24.8 and −24.9. These results indicate that the dissolved and particulate organic matter of the ship channel is rich in petrochemical carbon and that this material is diluted and replaced by natural marine carbon material with a less negative ratio as distance from Morgan Point increases.

The seasonal averages for Trinity Bay, when plotted against distance from the mouth of the Trinity River, reveal a somewhat different pattern (Fig. 7) than that of the Houston Ship Channel. Here, based on fish numbers, diversity decreases between the mouth of the river and Station 27. For fish weights, diversity decreases between Stations 25 and 24 and then gradually increases. Because of the large freshwater contribution of the Trinity River to the bay, the water at Station 25 remained fresh for most of the year. The salinity fluctuations encountered in other parts of the bay did not influence this area, leaving it less stressed than other parts of the bay. The occurrence of several freshwater species, combined with a more even distribution of individuals resulted in a more diverse population of fish supported in this area.

Because sampling was conducted for only one year, the effect on fish diversity of any great salinity variation in years of above average flooding can only be surmised. The immediate result of such flooding would be to flush the system and subsequently reduce pollution loading via dilution. However, salinity fluctuations increase the natural stress counteracting the reduced pollution stress so that an increase in diversity would not be expected.

Analysis of the trawl catches at the upper bay stations indicates that most of the species caught were represented by small individuals. It has been shown by Wohlschlag and Cameron (1967) that small fish are better able to withstand environmental stress than are large fish. This is due to the differences in metabolic rates between different size fish within the same species. Larger fish have less additional energy available to combat energy-requiring stresses because of the greater energy expenditure associated with the maintenance of a large biomass. Large fish are thus absent from the populations in an area subjected to stress, causing a more even distribution of biomass among the species with smaller individuals predominating. This is apparently the basis for the size distribution of species in an estuary as noted by Gunter (1961). Weight diversity is thus less influenced by changing environmental conditions in Trinity Bay and is apparently more or less equal throughout the bay. Conditions fluctuate to a greater extent as distance from the freshwater head increases, causing a steady decline in fish number diversity with distance in Trinity Bay.

The same relationship between diversity and distance from a source of pollution may be observed for the other stations in Galveston Bay as was shown to exist in the Houston Ship Channel and Trinity Bay.

Through the courtesy of TRACOR (Mr. Claude Ward, Project Leader), data indicating the dispersion of water in Galveston Bay, represented as a percent source of water at each sampling station, were obtained from a low-flow, conservative computer model (Table 10). The percentages for Houston Ship Channel Stations 3, 4 and 5 were not included in Table 10 because a two-dimensional program was used and stratification in the channel precludes the validity of such a model. Station 2 and those stations in West Bay, being under the influence of

TABLE 10

Computation of percent source of the entire volume of water at each station in Galveston Bay. Data provided by TRACOR from their flow model of Galveston Bay.

Station	% Bolivar Roads	% Trinity River	% Houston Ship Channel	% Other Water
1	74	7	14	5
15	47	16	33	4
16	49	9	18	24
17	50	9	18	23
18	43	16	37	4
19	28	16	55	1
20	24	14	61	5
21	13	9	78	0
22	26	15	58	1
23	24	42	36	0
24	20	54	28	0
25	16	63	22	0
26	21	52	29	0
27	23	48	31	0
28	31	34	37	0
29	37	27	37	0
30	35	27	38	0
31	51	9	17	23
32	49	9	17	25
36*	14	0	86	0

* Computed from salinity dilution, using average annual salinity for four depths in the Ship Channel; assuming the remainder to be made of Houston Ship Channel water.

water exchange through San Luis Pass, did not fit the model and were excluded from Table 10. Similarly, the model did not take the flow of Dickinson Bayou into account, making it necessary to exclude Station 37 from the table. The percentages for the remaining stations were used in subsequent sections for determining the source and amount of waste water at a station for comparison with species diversity indices.

The percent of water at any one station not attributed to either Bolivar Roads, Trinity River or Houston Ship Channel was assumed to be from some other input. Thus, the 24% and 23% other waters at Stations 16 and 17 are assumed to come from the Texas City waste disposal and the 23% and 25% other waters at Station 31 and 32 from the City of Galveston. Most of these inputs were known to contain wastes in various quantities and qualities.

If the percentages of Bolivar Roads and Trinity River waters are combined, the remaining amount of water must be from the Houston Ship Channel and other water sources. The relationship between the percent Houston Ship Channel waste water at any given point in the bay and diversity thus becomes a function of dilution and mixing of these water masses. Figures 8 and 9 reveal that there exists a linear relationship between the amount of toxic effluent entering via the Houston Ship Channel and the fish diversity of shallow stations in Galveston Bay exclusive of Trinity and East Bays. The y-intercept of the regression equation for

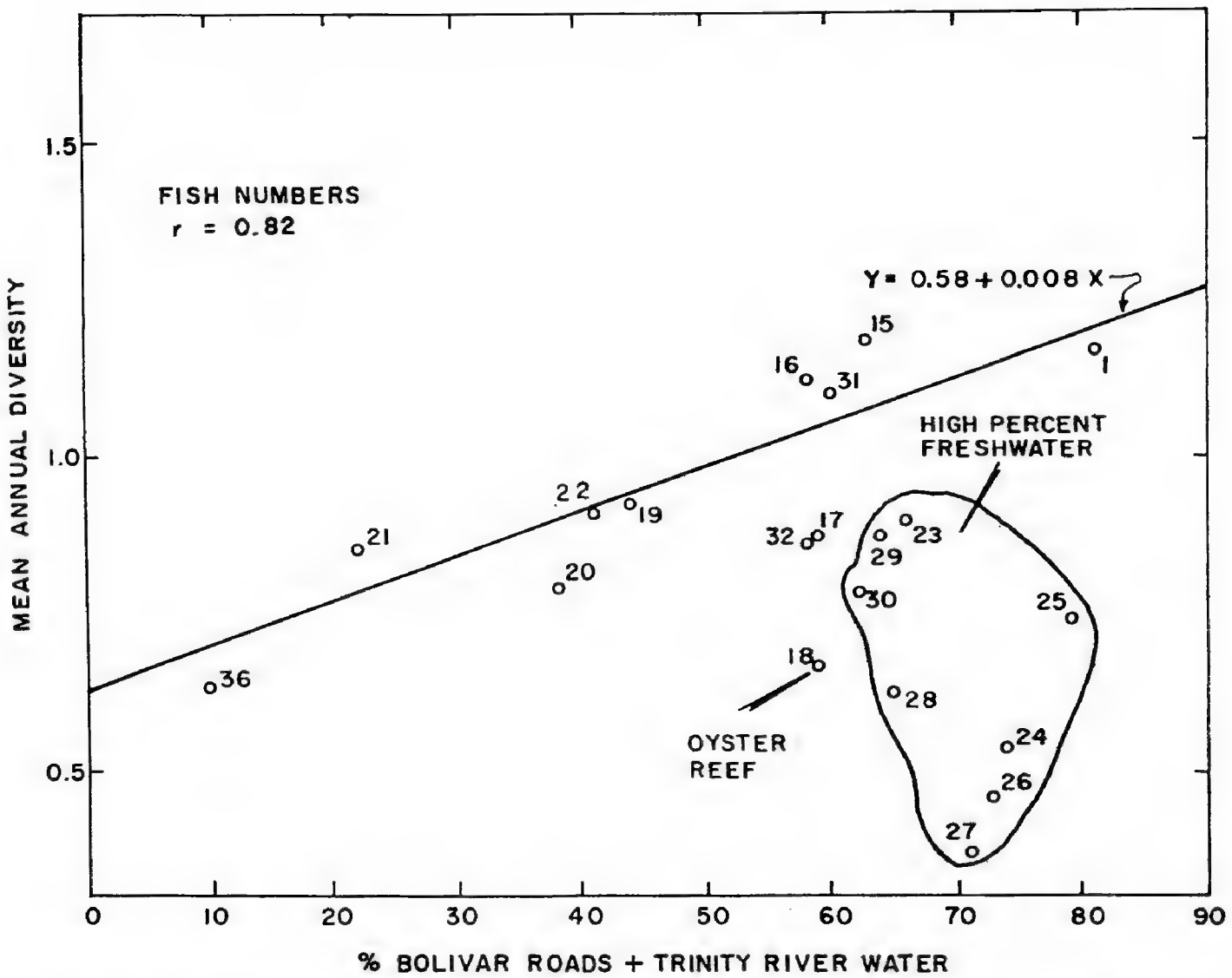

FIG. 8. Relationship between fish number diversity (natural bels/individual) and percent waste entering Galveston Bay via the Houston Ship Channel and other sources.

fish numbers ($y = 0.58 + 0.008X$) predicts that for the Houston Ship Channel above Baytown, Texas which can be considered to be 100% ship channel water, the mean annual fish number diversity should be 0.58. The mean annual diversity obtained at Station 36, which averaged 86% ship channel water during this study, was 0.620. For fish weights, the y-intercept of the regression equation predicts a diversity of 0.48. The mean annual diversity obtained at Station 36 was 0.633. It is thus apparent that the fish diversity of most of the shallow water stations of Upper and Lower Galveston Bay can be predicted if the fish diversity of the Houston Ship Channel above Baytown is known. If pollution loading increases along the industrialized section of the ship channel, the eventual effect on the fish diversity of the bay may be estimated.

The general trend in Galveston Bay has been such that as pollution loads have increased in the ship channel, more species of pollution-sensitive fish became physiologically unable to maintain themselves in the upper areas of the bay. As the environment further deteriorated, only the most pollution-tolerant species remained and became the dominant organisms in the community.

The diversity data indicate that serious water quality degradation has occurred in some sections of Galveston Bay. Trinity Bay and Upper Galveston Bay are stressed by both natural environmental fluctuations and pollution. The number

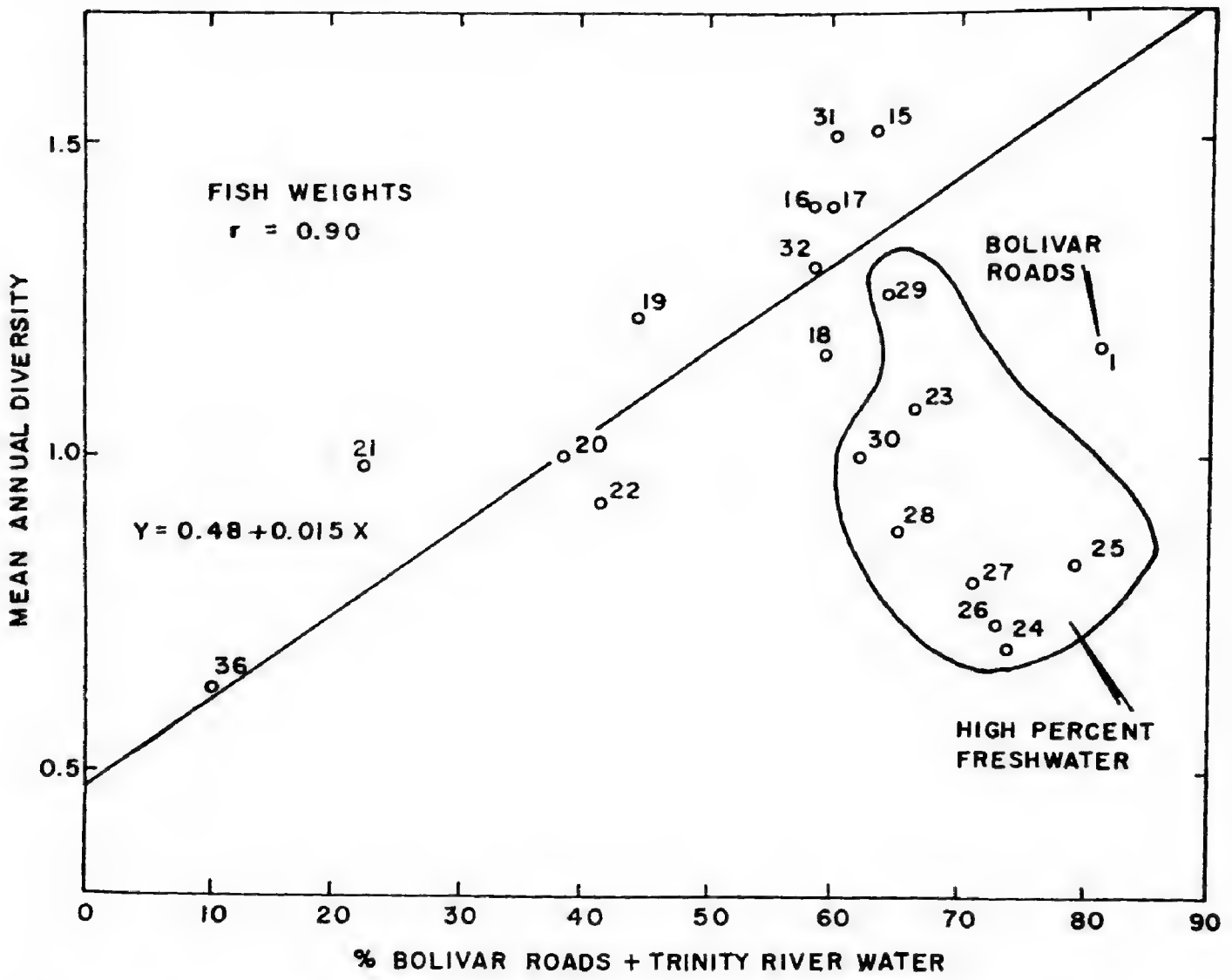

FIG. 9. Relationship between fish weight diversity (natural bels/individual) and percent waste entering Galveston Bay via the Houston Ship Channel and other sources.

of fish species occurring in these areas is reduced and the average size of the fish is smaller than those occurring in lower portions of the estuary. Most of the fish species which do occur are unspecialized feeders and are capable of wide adaptation.

An example is the anchovy which is predominantly a zooplankton feeder, but also utilizes detritus and microbenthic organisms. Increased pollution loading would probably not have a significant effect on the anchovy's food source, thus a relatively short food chain could be expected to be maintained in those areas having poor water quality.

Although the anchovy forms the basis for several sizable fisheries (Peru, West Africa), the question of whether the anchovy food chain is desirable in Galveston Bay should be ascertained. At present the anchovy population is not exploited. The anchovies caught during this study were not of commersial size, averaging less than 50 mm total length.

Apparently a food supply for larger fish can be maintained in the highly polluted waters, but it is not fully utilized because of the toxicity and stress problems for larger fish created by the pollution.

The effects of pollution in the upper portions of the Galveston Bay system have resulted in the need for an additional metabolic energy expenditure at the indi-

vidual organism level, resulting in smaller fish. On the community level, there is less energy for organization which is manifest in the lowered species diversity encountered in these areas.

CONCLUSIONS

It is becoming more apparent that one of the effects of estuarine pollution is a change in the structure of all trophic levels and thus of the entire estuarine community. Series of plankton and benthic communities characteristic of various levels of pollution in estuaries have been described. Within the limits of sampling conducted for this study, the diversity indices calculated did indicate populations of different diversities within the bay. It is also apparent that the fish populations of Galveston Bay can be divided into somewhat separate communities, structured as a response to environmental and pollutional stress. For example, Areas C, E and G are rather well separated geographically, but are similar in the type of fish communities they support (Table 1) and have no significant differences in diversity. The stations in these areas are all shallow and although influenced by different degrees of environmental and pollutional stress, have responded in such a manner as to support similar fish communities.

Copeland (1970) provides evidence that this type of response is not unique to Galveston Bay or to temperate estuaries. Bahia de Tallaboa, a tropical bay in Puerto Rico, supported a coral reef system of 160 species of fish until subjected to wastes from two small oil refineries. The net result of this stress was the elimination of the coral reef structure and a reduction of fish species to about 30, leaving the anchovy as the dominant species. If water quality conditions deteriorate in parts of Lower Galveston Bay so that several species of fish are eliminated, populations will become more similar in species composition and diversity to those of Upper Galveston Bay. The anchovy could very well become the dominant fish species throughout the bay system.

Considering the influence that the anchovy has on the diversity of a particular area, the scheme of assigning a dominance ranking to each area of the bay becomes more important when utilized as a long-range prediction tool. Does the predominance of anchovies in a particular area during a certain season indicate that water quality is becoming poorer, or is this occurrence a predictable part of the species life-history? Examination of Table 1 indicates that a dominance of anchovies in an area of Galveston Bay for more than two consecutive seasons would indicate that water quality in that area has deteriorated for there was no area in which the anchovy was the most abundant species for more than two consecutive seasons during this study.

Another result of deteriorated conditions, which would be evident only after a period of time, would be the absence of large fish in the area as they become unable to meet maintenance requirements due to stress.

Because very few diversity indices have been computed on fish catches, an accurate estimation of the state of health of Galveston Bay, as represented by the fish diversity of the bay, cannot be made. Margalef (1968) reported that the diversity of the demersal fish populations trawled along the Mediterranean

Spanish Coast ranged from 1.4 to 3.5. He noted that all values of diversity fell in a rather narrow range, with an upper limit near 4.5, representing an efficiency limit which aquatic communities may not be able to surpass.

The fish indices fall in the same range as do zooplankton and phytoplankton indices calculated as part of the Galveston Bay Study (personal observation). In studies of polluted waters using benthic macroinvertebrates to compute diversity indices, Wilhm and Dorris (1968) found that values less than one were obtained in areas of heavy pollution, values of one to three in areas of moderate pollution and values exceeding three in clean water areas. If the above values are used as a guideline, it is apparent that fish diversity indices can be used as a tool for stress analysis and do reflect areas of pollution in Galveston Bay. The fish diversity indices calculated for this study indicate that Galveston Bay is heavily stressed by pollution and environmental factors in the upper areas and moderately stressed in the lower parts. Trinity Bay and most parts of Upper Galveston Bay, especially the Houston Ship Channel above Morgan Point, are unable to support diverse fish communities for other than short periods of time. Fish diversity in this area can be used to predict diversity in the bay because of the linear relationship between distance and dilution of the ship channel effluent. Increased waste loading of the Houston Ship Channel above Morgan Point will have a predictable, deleterious effect on the fish populations of this important Texas estuary.

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NEARSHORE SURFACE CURRENTS, SOUTHEASTERN TEXAS GULF COAST

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The University of Texas Marine Science Institute at Port Aransas, Texas

ABSTRACT

Thirteen monthly releases of drift bottles at 18 stations along the Texas Gulf Coast offshore from Mustang and Padre Islands indicate that the nearshore surface circulation in depths of eight fathoms and less is strongly influenced by the local wind circulation. During the summer months of strong southerly winds, the bottles drift to the north along the shoreline. In the winter months characterized by alternating northerly winds of frequent winter storms and the prevailing southerly winds, bottles drift either north or south along the shoreline depending on the winds active during and immediately preceding their drift at sea. Anomalous southerly drift often occurs during tmies of transition between winter and summer wind regimes.

INTRODUCTION

Several lines of evidence suggest that nearshore currents and littoral drift have a net annual convergence in the vicinity of central Padre Island. This is reasonable insofar as these currents are wind derived. The wind regime in this area is bimodal with north to east winds accompanying Arctic and Pacific cold fronts during fall and winter and onshore, south to southeasterly, trade winds prevailing during spring and summer (Fig. 1). Since a wind vector meeting a coast at any oblique angle would have a longshore as well as an onshore component, a vector which is perpendicular to the coast indicates current convergence on a concave coast. And the annual resultant vector based on velocity, duration and direction is perpendicular to the central Texas coast approximately at Port Aransas.

The currents generated by winds exist as water translated alongshore seaward of the surf zone and as longshore currents in the surf zone generated by oblique wave approach. The second process results in longshore transport of sand and coarser sediment; and its net effects can be interpreted from characteristics of sediment distribution, erosion and accumulation. Distribution of heavy mineral suites (Bullard, 1942; Van Andel and Poole, 1960), sand size modes (Hayes, 1965), and shell material (Watson, 1968) all indicate a littoral drift convergence zone on central Padre Island. Pelecypod valve sorting also can be related to direction of wave approach. Although shell sorting trends cannot be correlated

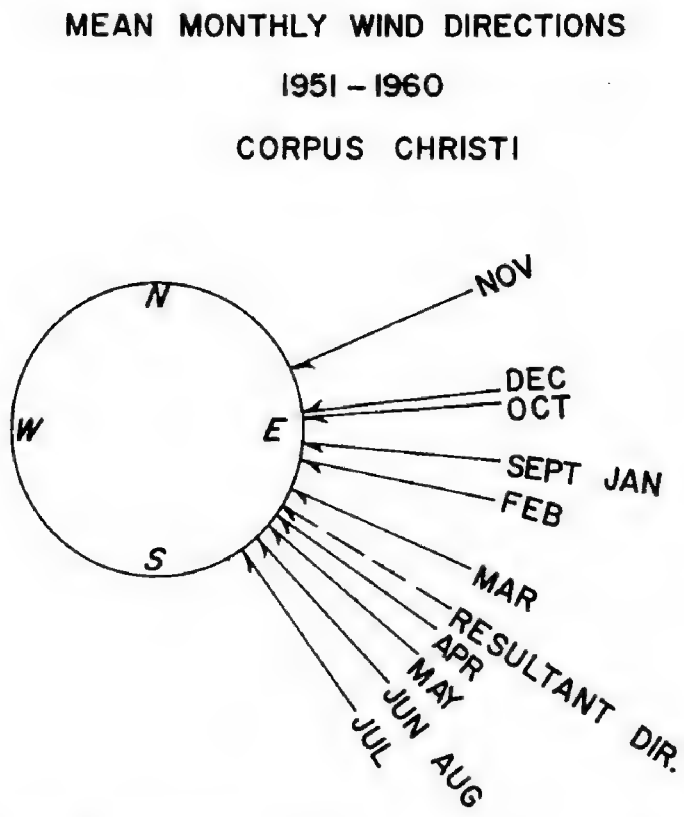


FIG. 1. Mean Monthly Wind Directions for Corpus Christi 1951–1960. Directions shown represent the average of the monthly vector resultants determined for 10 years of wind data collected at Corpus Christi. The RESULTANT DIR. shown is the vector sum for the entire 10 year period. Vector magnitudes are calculated as a vector product of velocity, duration, and direction.

quantitatively with littoral drift, they do reflect the seasonal fluctuations in the wind-wave regime (Behrens and Watson 1969, Table 2).

The purpose of this study was to measure surface water movement on the shallow shelf beyond the surf zone in order to determine whether or not currents in this region reflect the convergence deduced from the beach sediment characteristics. The area of study was restricted to the sandy bottom, barrier shore-face between depths of three and eight fathoms.

Currents on the continental shelf have been studied both by direct current meter measurements and by drift bottle studies. Drift bottle techniques were used by Kimsey and Temple (1962, 1963) in a study of currrents on the entire continental shelf between the mouths of the Mississippi and Rio Grande Rivers. Again, a seasonal shift was observed with west to southerly flowing currents being driven by north to easterly winds during the winter regime and north to easterly flowing currents being driven by summer southerly winds. Littoral drift driven by waves generated by these same winds could produce the net convergence observed in the sediments. Transitional periods between the summer and winter regimes were often characterized by onshore winds and actual nearshore current convergence on the central Texas coast.

Counter currents against the prevailing wind conditions were sometimes indicated along the south Texas coast by data from the four stations nearest shore in this area. However, only two of these stations were inside the eight-fathom con-

tour. It was hoped that the present study would reveal more of the nature of this counter current.

PROCEDURE

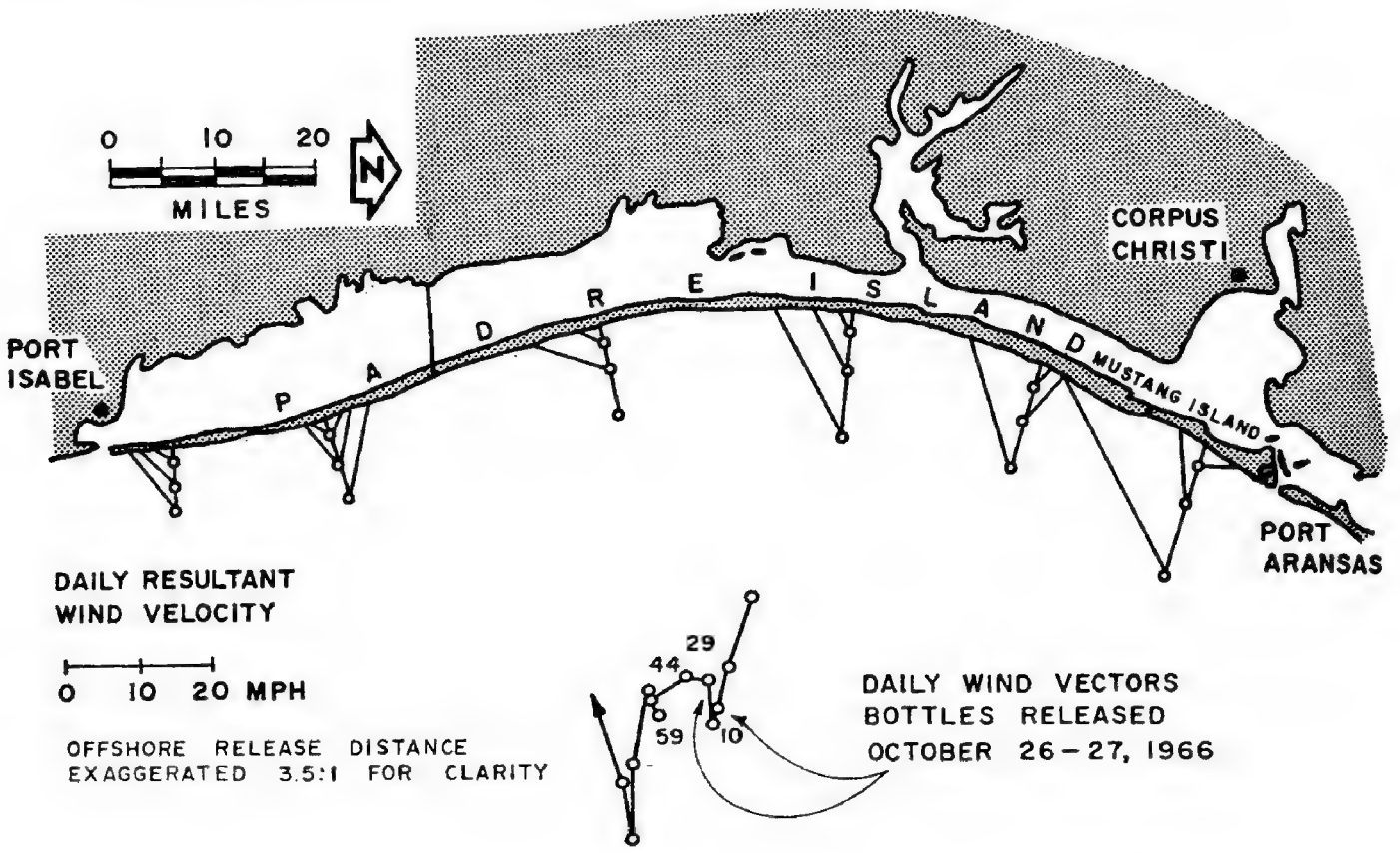
Unweighted drift bottles were released monthly at 18 stations off the Texas coast between Port Aransas and Port Isabel. Releases were made approximately monthly from October, 1966 through December, 1967. The bottles were released along six traverses perpendicular to the shoreline at distances corresponding to depths of three, six and eight fathoms. In October, 1966, five bottles were released at each station. Recoveries that month were so high that in all succeeding releases only two bottles were dropped at the two fathom station and three each at the six and eight fathom stations.

For the first four months bottles were released from boat over a cruise period of two days. Subsequently bottles were released from a light plane within a four-hour period.

RESULTS

Figures two through fourteen summarize all of the surface current data gathered during the study period. Each map shows the three, six and eight-fathom release stations along each of the six traverses perpendicular to the shoreline. The distance from shore of the plotted release points is exaggerated for clarity. The lines drawn from the release points to the shoreline represent the shortest path that the bottles could have traveled from their release to the location at which they were found on the beach. Wind records collected by the Weather Bureau Office at Corpus Christi, Texas, were used to plot the vectors of daily wind velocity. The arrow at the end of the plot of vectors indicates the direction toward which the wind was blowing. The small arrows pointing to one or two days on the plot of daily wind vectors indicate the day or days on which the drift bottles for that month were released. The numbers plotted alongside of the wind vectors indicate the cumulative number of bottles found up to and including that day. For instance, on the releases for November 30 and December 1, 1966 (Fig. 2), eight bottles were found by December 2 and 30 bottles were found by December 7.

Qualitative analysis of these records reveal two trends. First, during most months (nine out of 13) the bottles drifted in the direction of the alongshore component of the local wind. Bottle drift direction was better than 90% predictable during these times. The correlation with local winds follows the bimodal pattern of southerly drift in response to northerly winter winds and northerly drift in response to southerly summer winds (note especially October, 1966; July, August, September and December, 1967). During two months (November, 1966 and February, 1967) local winds were easterly enough to produce an immediate convergence on central Padre Island where sediment relations indicate a net annual convergence of littoral drift. Wind shifts shortly after the drops made in December, 1966 and January, 1967 produced somewhat more complex but not particularly anomalous patterns of drift.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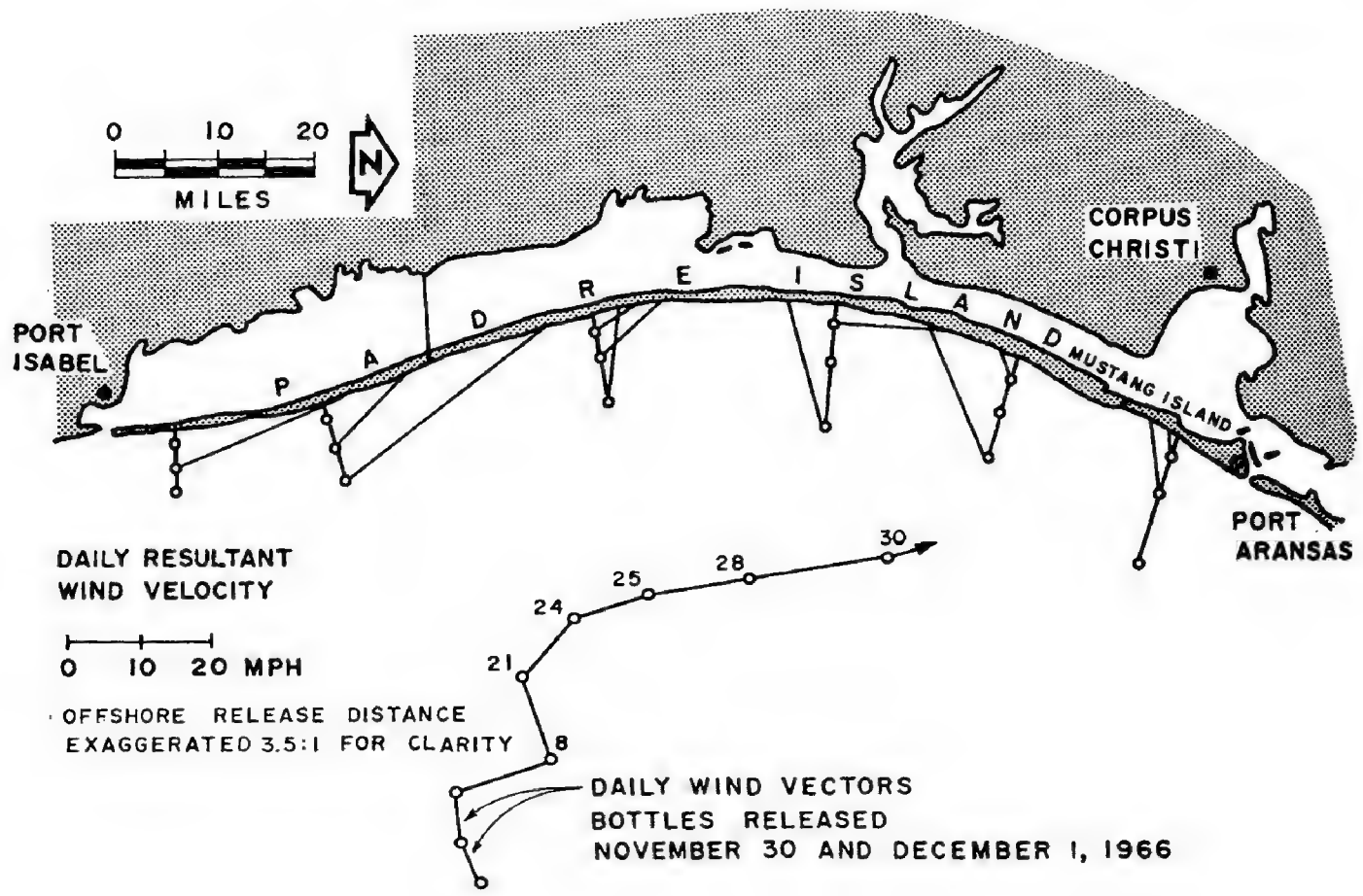
MILES
N
CORPUS CHRISTI
PORT ISABEL
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
29
44
59
10
DAILY WIND VECTORS
BOTTLES RELEASED
OCTOBER 26–27, 1966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MILES
N
CORPUS CHRISTI
PORT ISABEL
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MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
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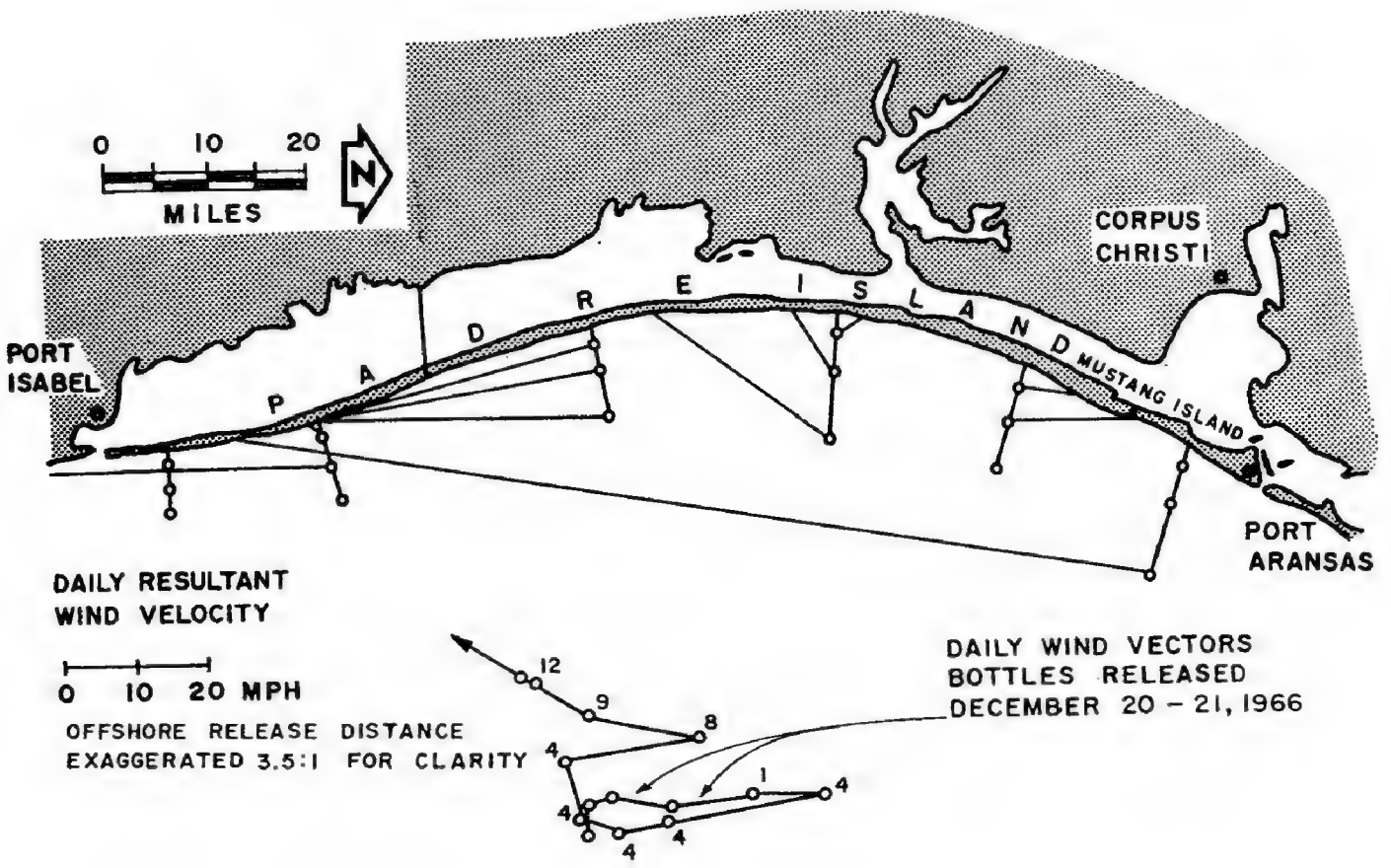
28
25
24
21
8
DAILY WIND VECTORS
BOTTLES RELEASED
NOVEMBER 30 AND DECEMBER 1, 1966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N
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MUSTANG ISLAND
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PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
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9
8
4
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4
1
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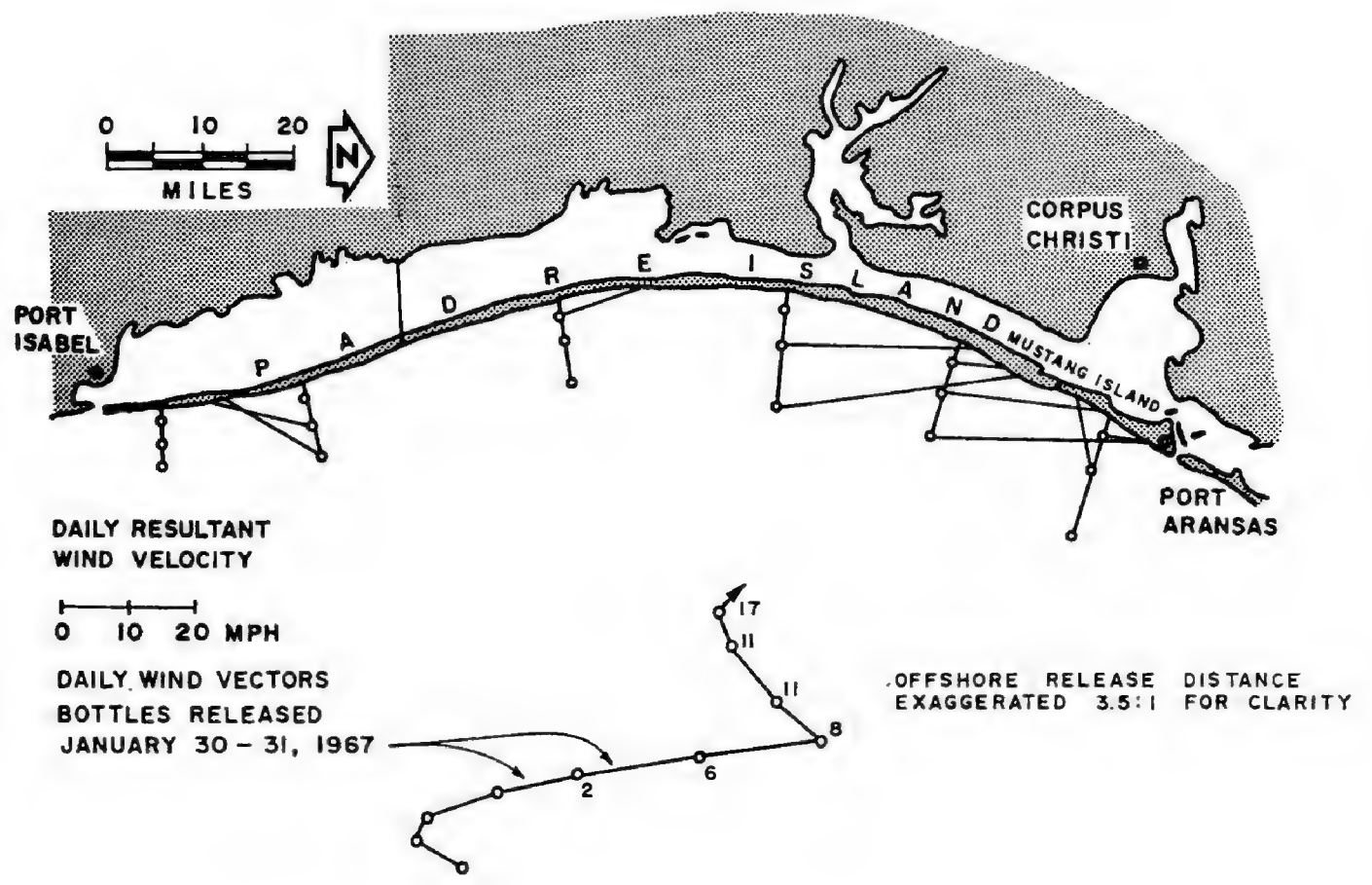
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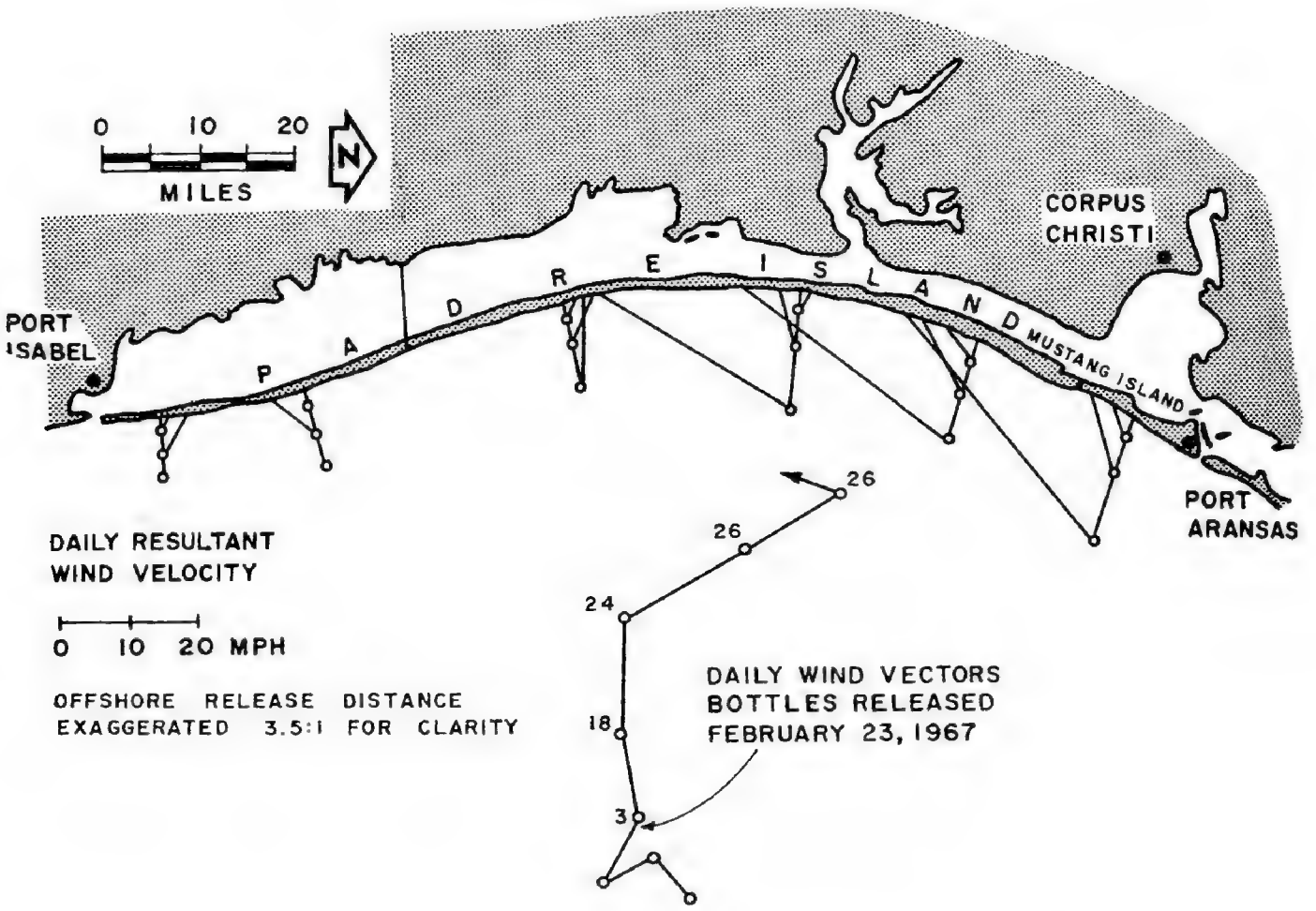
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
DAILY WIND VECTORS BOTTLES RELEASED JANUARY 30 – 31, 1967
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
17
11
11
8
6
2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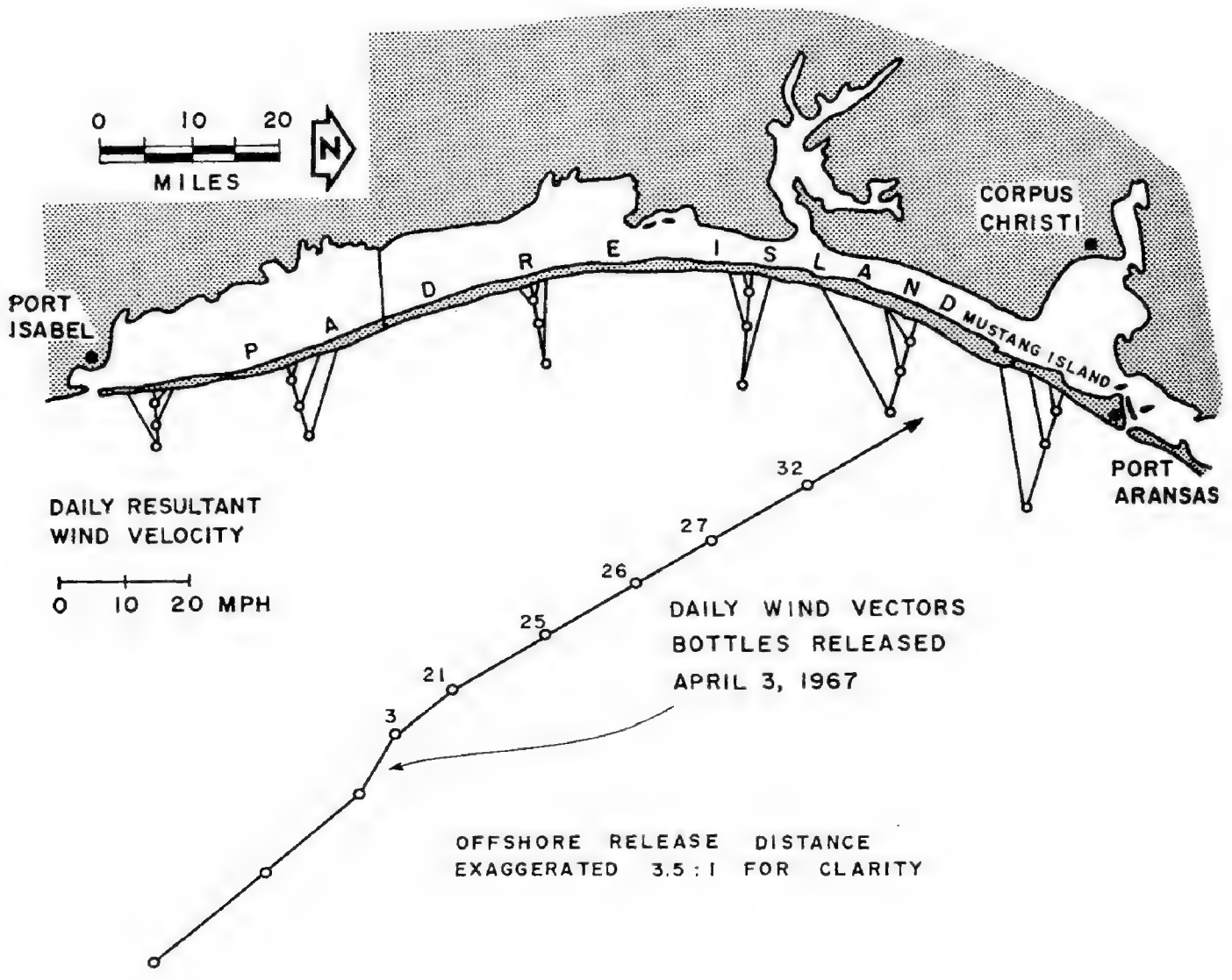
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
26
26
24
18
3
DAILY WIND VECTORS
BOTTLES RELEASED
FEBRUARY 23, 1967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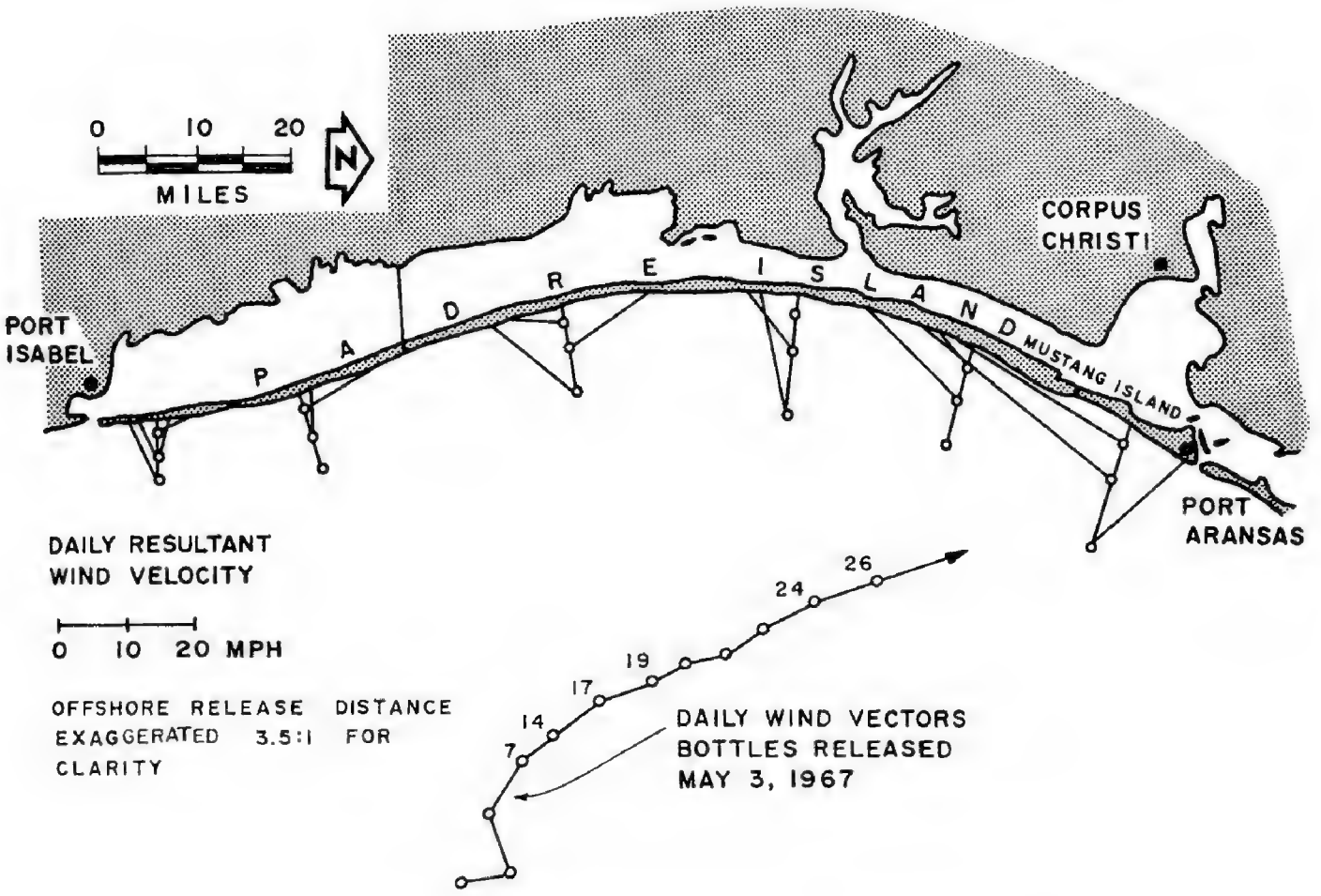
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5 : 1 FOR CLARITY
32
27
26
25
21
3
DAILY WIND VECTORS
BOTTLES RELEASED
APRIL 3, 1967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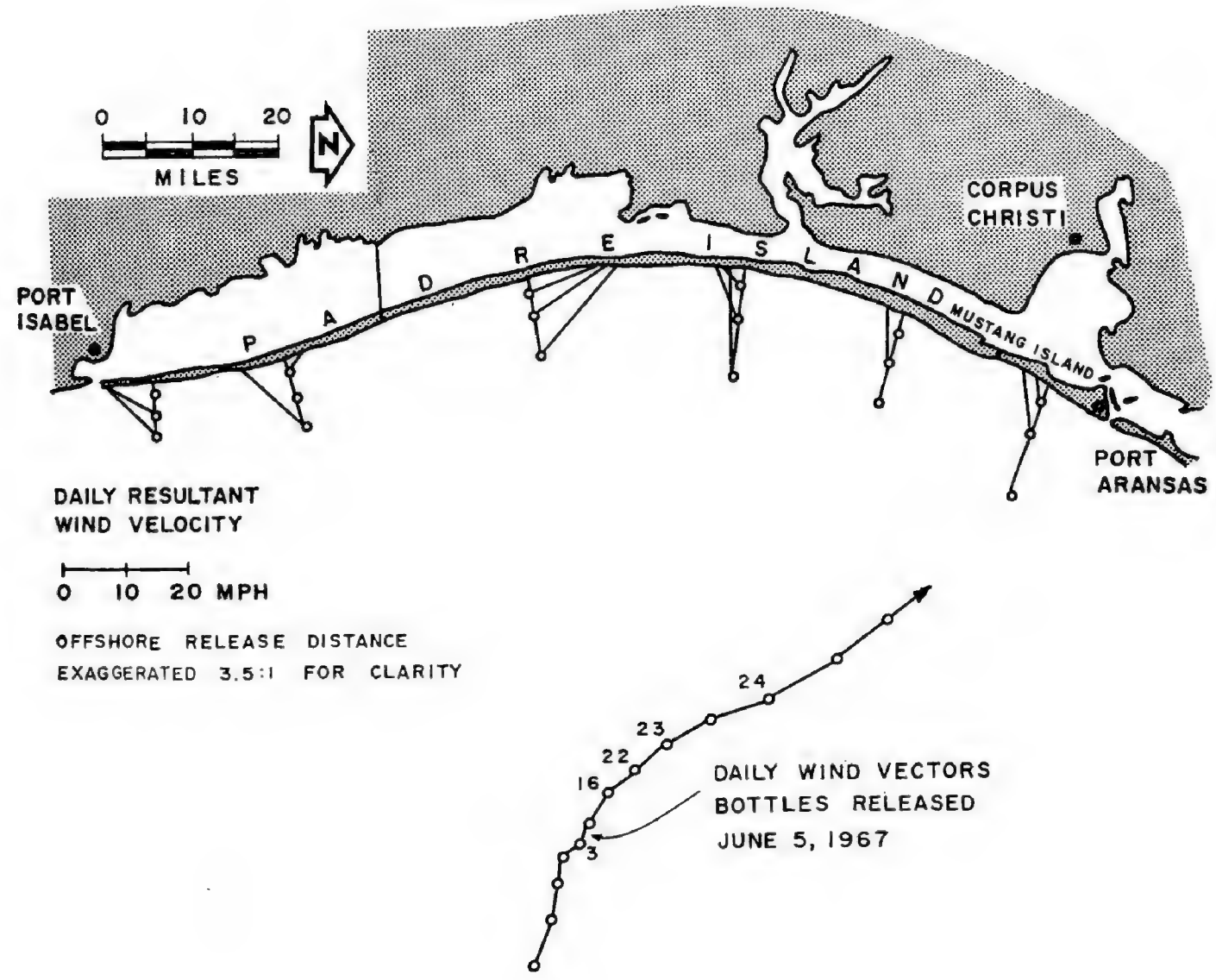
CORPUS CHRISTI
PORT ISABEL
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
26
24
19
17
14
7
DAILY WIND VECTORS BOTTLES RELEASED MAY 3, 1967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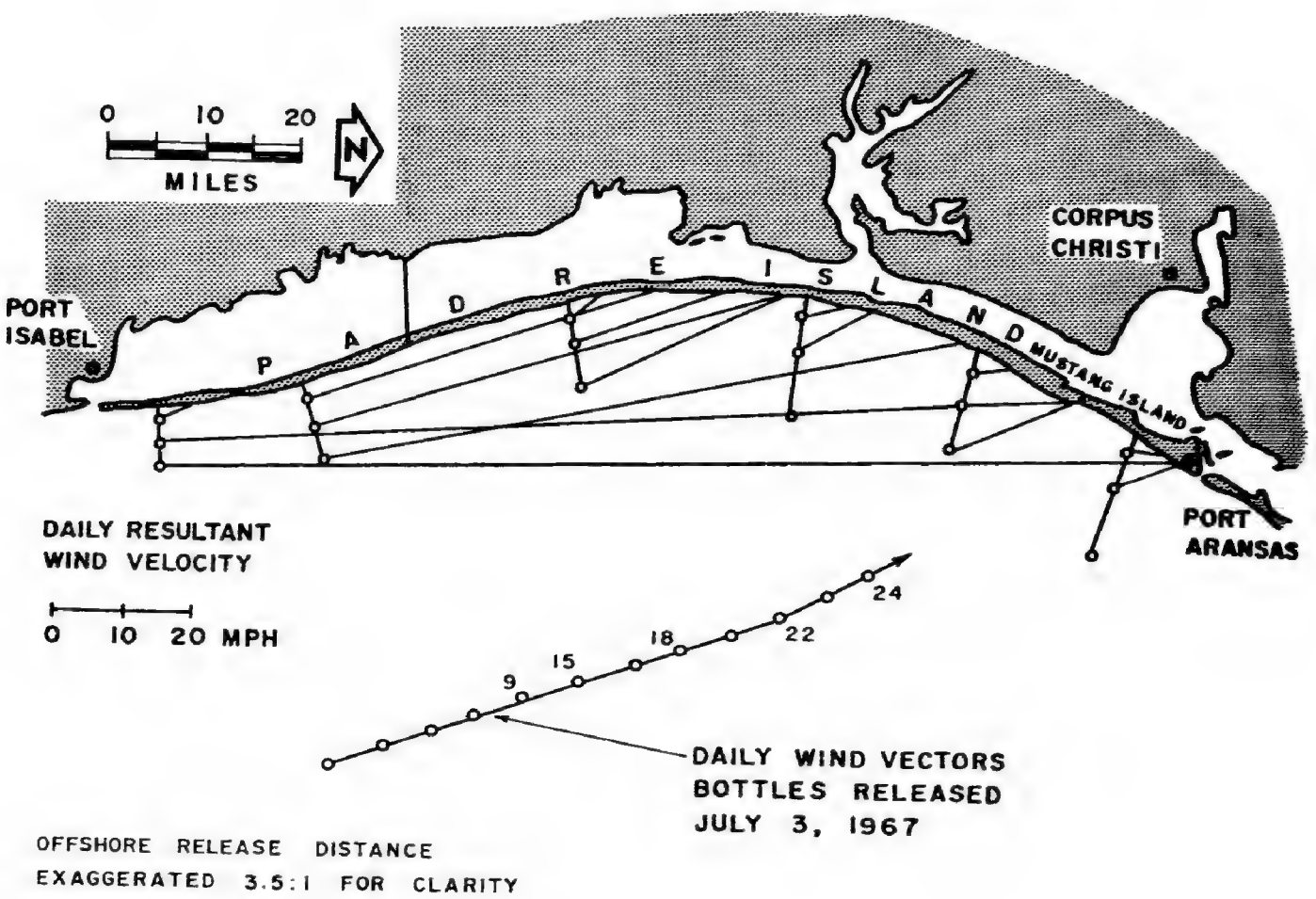
CORPUS CHRISTI
PORT ISABEL
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
24
23
22
16
3
DAILY WIND VECTORS BOTTLES RELEASED JUNE 5, 1967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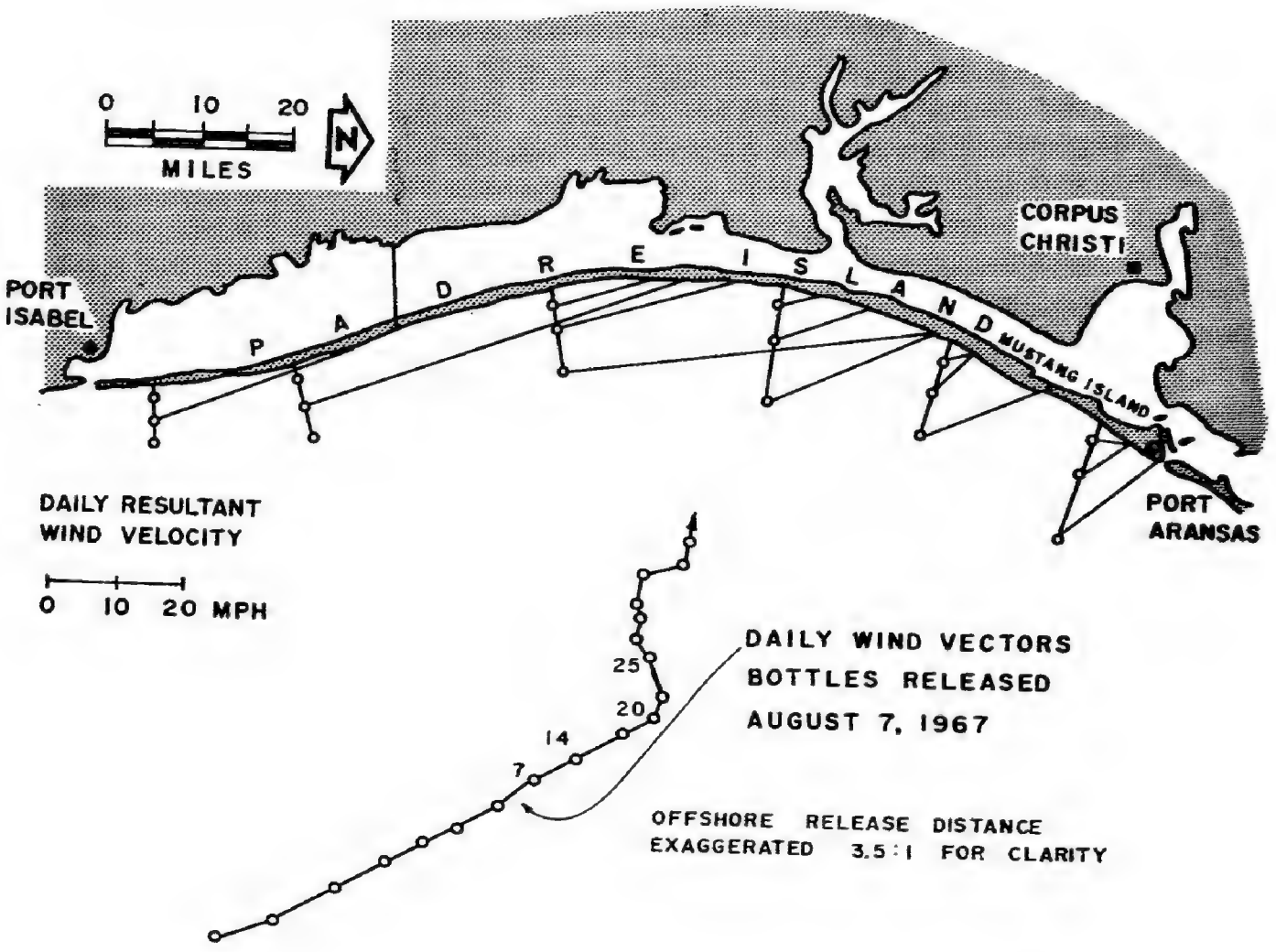
CORPUS CHRISTI
PORT ISABEL
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
9
15
18
22
24
DAILY WIND VECTORS
BOTTLES RELEASED
JULY 3, 1967
OFFSHORE RELEASE DISTANCE
EXAGGERATED 3.5:1 FOR CLARITY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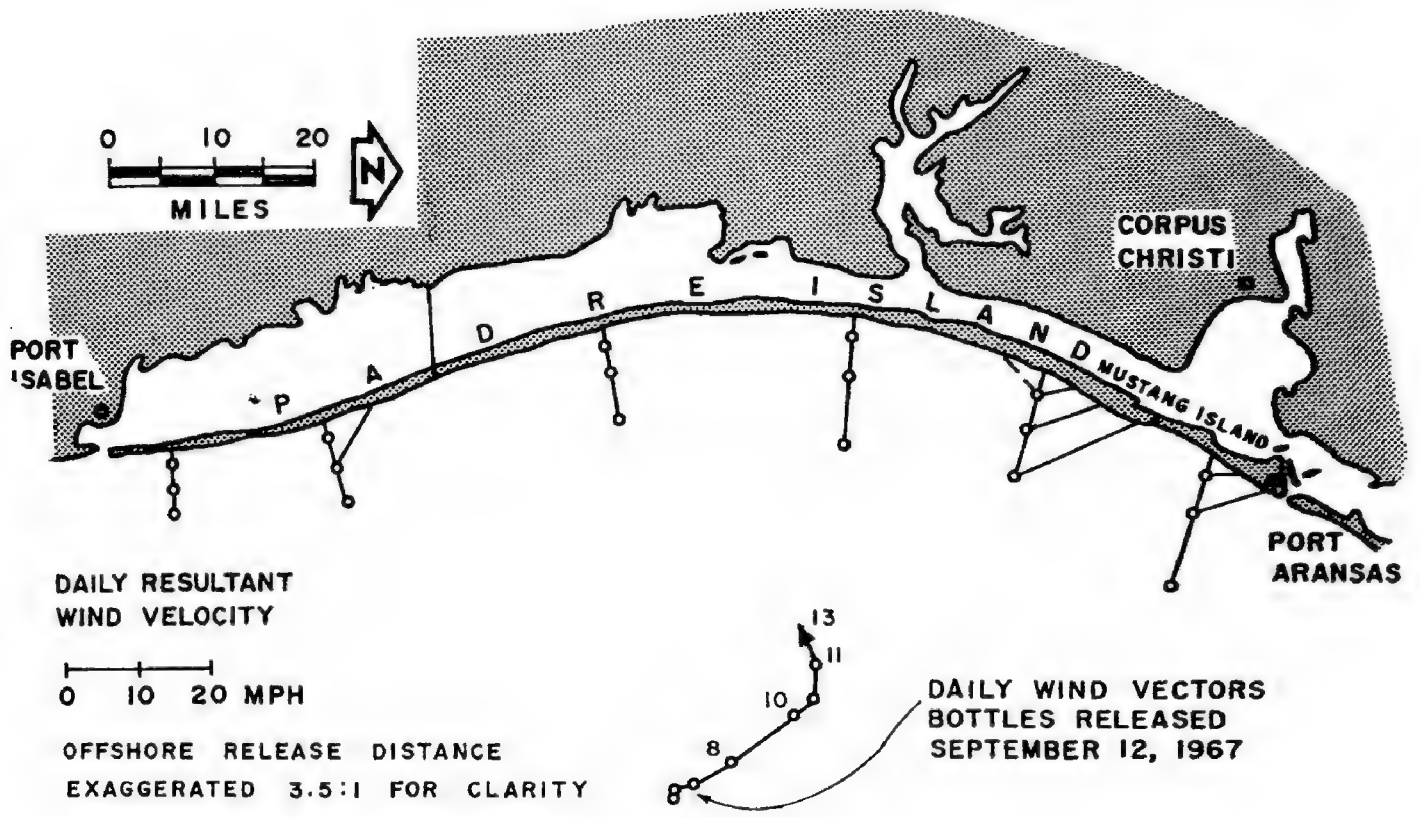
PORT ISABEL
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
7
14
20
25
DAILY WIND VECTORS
BOTTLES RELEASED
AUGUST 7, 1967
OFFSHORE RELEASE DISTANCE
EXAGGERATED 3.5:1 FOR CLARITY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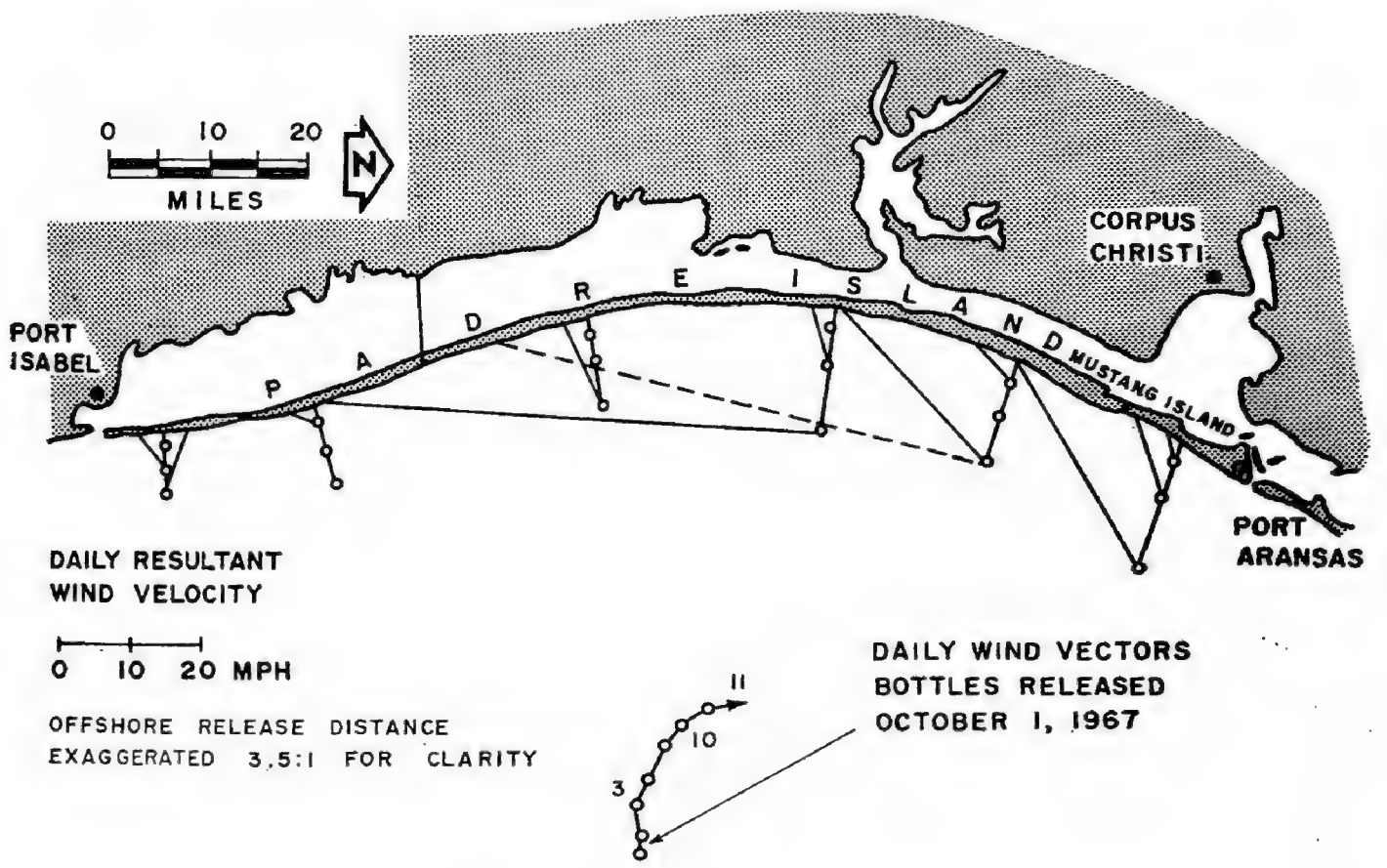
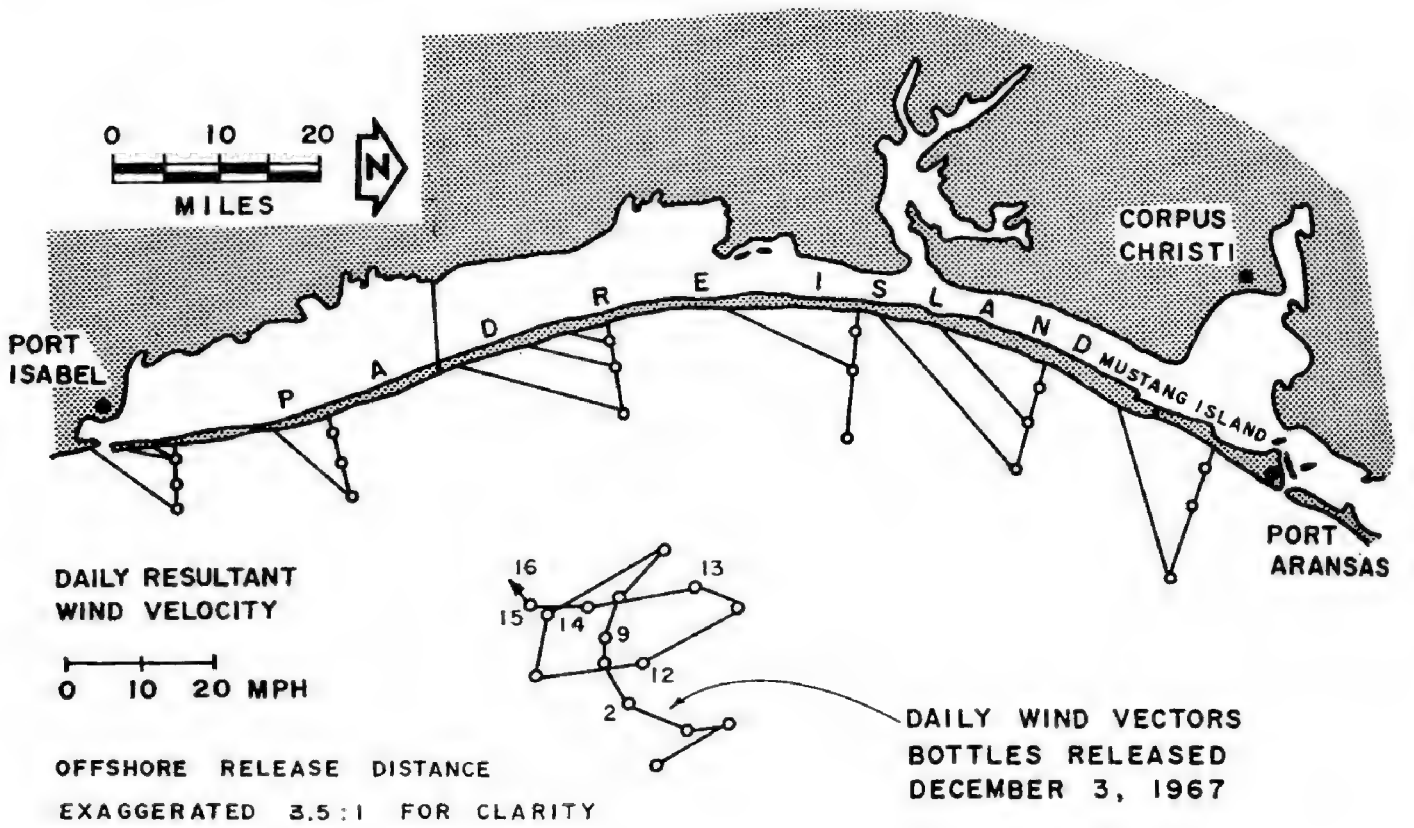
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
13
11
10
8
DAILY WIND VECTORS BOTTLES RELEASED SEPTEMBER 12, 1967


0 10 20
MILES
N
CORPUS CHRISTI
PORT ISABEL
PADRE ISLAND
MUSTANG ISLAND
PORT ARANSAS
DAILY RESULTANT WIND VELOCITY
0 10 20 MPH
OFFSHORE RELEASE DISTANCE EXAGGERATED 3.5:1 FOR CLARITY
11
10
3
DAILY WIND VECTORS BOTTLES RELEASED OCTOBER 1, 1967



The second major observation is that during four months transitional between summer and winter wind regimes (April, May, June and October, 1967) there was significant drift against the prevailing local winds. Only about 35 to 40% of the bottles drifted as would be predicted. In all cases southerly drift predominated while northerly drift should have prevailed at all stations. This anomalous drift during the spring months resulted in a convergence on central Padre Island. This drift is opposite in direction to the counter current observed off southern Padre Island by Kimsey and Temple (1963).

DISCUSSION AND CONCLUSIONS

Drift bottle movements observed in this study indicate that most of the currents on the shallow shelf off Mustang and Padre Islands, Texas can be generated by local winds as measured in Corpus Christi. Nearshore currents flow in opposite directions during winter and summer just as do the prevailing winds. During periods of transitional weather, especially in the spring, southward surface drift is often counter to the local southerly winds. Apparently this area is affected by significant currents generated by winds representative of winter conditions in another, probably more northern part of the Gulf while summer winds have begun to or are still blowing in the south Texas region.

Both beach sediment distribution and the net annual wind vector for Corpus Christi indicate that net annual littoral drift converges along the central Texas coast; but the sediment distribution indicates the nodal point is on central Padre Island while the wind data suggests that it is on northern Mustang Island.

This study shows a similar convergence of nearshore surface currents. The similarity between nearshore surface currents and littoral drift along the Texas

coast is not surprising since both are primarily generated by local winds. The littoral drift is driven primarily by waves generated from local winds and secondarily by waves from distant storms while the nearshore surface currents are also driven primarily by local winds, they are apparently driven secondarily by some other circulation system active principally during spring months.

ACKNOWLEDGMENTS

We wish to thank The United States Department of the Interior Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory at Galveston, Texas for providing the drift bottles and paying rewards to the many individuals who found and reported drift bottle landings. We especially appreciate the cooperation of Milton J. Lindner, Robert F. Temple, and Kenneth N. Baxter of that Laboratory. Mr. John Batterton was kind enough to act as pilot for many of the bottle release flights. Mrs. Judith Watson drafted the figures.

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THECAL MORPHOLOGY OF SELECTED SPECIES OF *DINOPHYSIS* (DINOFLAGELLATA) FROM THE GULF OF MEXICO

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Department of Oceanography, Texas A&M University, College Station, Texas 77843

ABSTRACT

Detailed descriptions of the thecal plates of 10 species of the genus *Dinophysis*, one of which is new, are given. Discovery of an additional, small plate necessitates a new plate formula: 6E (epithecal), 4C (cingular), 4H (hypothecal), and 4S (sulcal). The question arises as to whether all species of *Dinophysis* have these 18 plates. The type species, *D. acuta* Ehrenberg, has priority in establishing the plate formula for the genus.

INTRODUCTION

Recent literature dealing with the systematics of dinoflagellates only has begun to accomplish what is needed to adequately describe and classify individuals within the group. Advances such as electron microscopy provide new areas for concentrated effort, yet old and basic taxonomic problems remain which confound the student. The main objectives of the present report are: (1) to carefully study and describe representatives of the "hastata" group of the genus *Dinophysis* which are present in the Gulf of Mexico, and (2) to attempt to ascertain from field samples whether there are definitive morphological criteria by which the species in this group can be delimited.

After the establishment of *Dinophysis hastata* Stein (1883), about 25 closely related species have been described which could be placed in a "hastata" group. A brief definition of this group is given by Kofoid and Skogsberg (1928: 237): "Body of varied shape, rounded, ovate, subovate, or rounded subtrapeziform in lateral outline, without posterior peduncle. With one or two posterior sails and sometimes with parasagittal lists along dorsal side of hypotheca." Earlier reports of this group are reviewed in Kofoid and Skogsberg (1928). Significant taxonomic contributions since have been added by Tai and Skogsberg (1934) and Balech

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(1967c). Papers with less descriptive detail are those of Dangeard (1927), Schiller (1928), Pavillard (1931), Böhm (1936), Rampi (1940, 1950), Gaarder (1954), Wood (1954, 1963), Silva (1956, 1958), Hasle (1960), Halim (1960, 1967) and Abé (1967a,b).

Kofoid and Skogsberg (1928: 236) list the following fourteen species as members of the "hastata" group: *Dinophysis alata* Jörgensen, *D. collaris* Kofoid and Michener, *D. hastata* Stein, *D. jörgenseni* Kofoid and Skogsberg, *D. monacantha* Kofoid and Skogsberg, *D. nias* Karsten, *D. pusilla* Jörgensen, *D. rudgei* Murray and Whitting, *D. schuetti* Murray and Whitting, *D. swezyi* Kofoid and Skogsberg, *D. trapezium* Kofoid and Skogsberg, *D. triacantha* Kofoid, *D. uracantha* Stein and *D. urceolus* Kofoid and Skogsberg. The translation of *Phalacroma* to *Dinophysis* (Abé 1967b: 38; Balech 1967c: 82–84) adds seven species to this list: *D. circumsuta* (Karsten) Balech, *D. cuneolus* (Kofoid and Skogsberg) Balech, *D. doryphorides* (Dangeard) Balech, *D. doryphora* (Stein) Abé, *D. paulseni* (Schiller) Balech, *D. pugiunculus* (Jörgensen) Balech and *D. pulchra* (Kofoid and Michener) Balech. Other members of the "hastata" group are: *D. capitulata* Balech (1967c), *D. odiosa* (Pavillard) Tai and Skogsberg (1934), *D. reticulata* Gaarder (1954) and *D. spinosa* Rampi (1950).

Dinophysis hastata is considered to be a collective species by Kofoid and Skogsberg (1928: 266), Abé (1967b: 77) and Balech (1967a: 282). The variations in this species, 20 of which are illustrated in Kofoid and Skogsberg, Figs. 32 and 33, also indicate a need for further study. Tai and Skogsberg (1934: 452) state ". . . not only is a thorough revision of *Dinophysis hastata* urgently needed; all the other species belonging to the general group . . . should be subjected to a re-evaluation." Furthermore, the descriptions of some members of the "hastata" group, *viz, D. monacantha, D. trapezium* and *D. urceolus* are based on only one or two individuals, hence, their variations are virtually unknown and their validity is open to question.

Discussions concerning analyses of the thecal morphology in the tribe Dinophysoidae are reviewed by Norris (1969). Briefly, it may be said that the number and arrangement of the thecal plates are considered to be basic taxonomic features. Thecal plate analyses have been made on only four members of the "hastata" group, the first by Tai and Skogsberg (1934: 448) on *D. odiosa*; the others, *D. paulseni, D. pusilla* and *D. capitulata* by Balech (1967c).

Tai and Skogsberg (1934: 414) were the first to emphasize the significance of the plate pattern in the Dinophysoidae and list three outstanding characteristics for it in *Dinophysis*: (1) all four sulcal plates border the flagellar pore; (2) both ventral hypothecal plates are small and elongate, arranged one behind the other, with their long axes in the longitudinal plane; and (3) the two ventral epithecal plates are similar in shape, size and position.

Abé (1967a: 375) confirms this arrangement of the ventral epithecal plates but he has found an exception in the arrangement of the ventral hypothecal plates within the family Dinophysidae. This has led him to attach considerable significance to the arrangement and the relative or total length of these plates, and to devote much effort to their analysis. In regard to the sulcal plates, Abé

(1967a: 381) agrees with the number and arrangement ascertained by Tai and Skogsberg (1934).

Work on dinoflagellate taxonomy in the Gulf of Mexico has been limited, especially in the oceanic region. The most comprehensive contribution is by Balech as a result of studies in 1964–65 (1967a, b, c); he also gives the most complete review (1967b). Recent oceanic work is by Norris (1969). Significant contributions are being made from estuarine and neritic regions, *e.g.*, Steidinger *et al.* (1967) and Steidinger (1968). Wilson (1967) has a paper resulting from culture studies.

The present paper contributes to the clarification of the descriptions of ten members of the "hastata" group found in the Gulf of Mexico. While the general descriptions in this paper are similar to those in previous works, their presence supplements the illustrations and enables one to make comparisons of the species taken at different times and places. Analyses of the plates of three species, *viz*, *D. odiosa*, *D. paulseni* and *D. pusilla* supplement previous efforts and reveal variations within these species. Individuals of seven species have been dissected and their plates described for the first time. A limited list of synonyms is given for each species, for additional listings reference is made to Kofoid and Skogsberg (1928). In addition, this paper presents data on the distribution of these organisms.

MATERIALS AND METHODS

The 51 samples used for this study were taken on three cruises of R/V ALAMINOS (Fig. 1): 66-A-5 (March 1966), 67-A-5 (July 1967), and 68-A-4 (April 1968). Water was filtered through a 35 μ-mesh microplankton net via various methods. The net has a mouth diameter of 18 cm and an overall length of 122 cm. Surface and 10 m and 100 m vertical hauls were taken on the first cruise (designated MP for microplankton); on the second cruise samples were collected by attaching the microplankton net to the cod end of a "Bongo" opening and closing net towed at various depths (designated BN for Bongo-net); and on the last cruise samples were taken by filtering water pumped from various depths and via surface tows (designated P for pump samples). All samples are preserved in 10% formalin.

A standard bright-field compound microscope was employed in the microscopic analyses. Only one opportunity was afforded to examine a specimen under phase-contrast. It was found that phase-contrast greatly facilitates seeing suture lines and should be employed when feasible, it is especially helpful in observing the pore platelet referred to later.

Small quantities (ca. 1 ml) of the settled plankton were examined under 100x magnification and individuals were removed via a micropipette and stored in glycerin for further examination. This procedure was repeated until no apparent different species appeared in the fraction. The species were tabulated by cruise and sample (Table 1) and by depth (Table 2). In all, 77 specimens of the 10 species found were studied closely in order to elucidate variations. Dissections were made of 44 of these individuals in order to analyze the plate pattern and the thecal morphology. Measurements were made using an ocular micrometer following the methods of Kofoid and Skogsberg (1928: 208). Additional measurements taken were: transdiameter, across the base of the cingulum in ventral view; R_1—R_2 x(y), where x is the distance between the anterior main rib (R_1) and the fission rib (R_2) at their bases, and y is the distance between these ribs distally; R_2—R_3, as above but between the fission rib (R_2) and the posterior main rib (R_3); R_3—PS, as above but between the posterior main rib (R_3) and the posterior sail (PS). All measurements given under *Dimensions* for each species are in microns (μ).

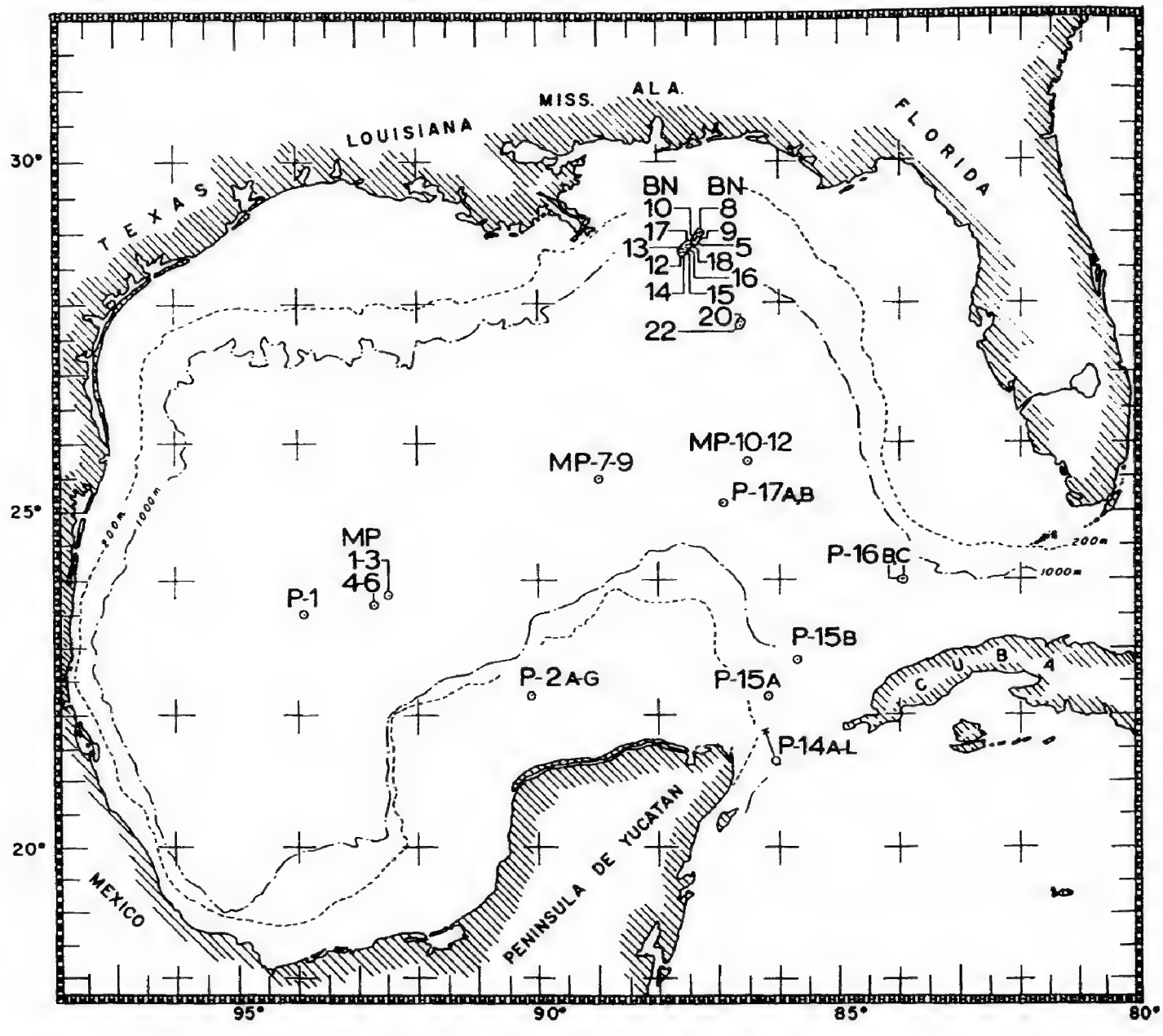


FIG. 1. Chart showing collection sites. BN = Bongo-net samples; MP = microplankton samples; P = pump samples

Methods followed in the plate analyses are described by Tai and Skogsberg (1934: 385–386) and Graham (1942: 3–4) and are briefly given by Norris (1969). Dissection of individuals was carried out under oil immersion. The plate terminology is that of Tai and Skogsberg, as modified by Balech (1967c and personal communication). Principal features and the plates of *Dinophysis* are illustrated in Figures 2–8. Drawings were made with the aid of a camera lucida.

SYSTEMATIC ANALYSES

Dinophysis Ehrenberg, 1840

General Discussion of Thecal Plates

As indicated in the introduction, previous studies of the thecal morphology in the Dinophysoidae are built on the classic work of Tai and Skogsberg (1934). The present study also has relied on this paper; however, it has revealed a significant omission in all previous works dealing with plate analyses of *Dinophysis*. Herein is reported for the first time the presence of an additional plate. The 10 species examined in this study are consistent in having the plate. Thus, the theca of the

TABLE 1

List of Dinoflagellates Examined and Record of Occurrence by Cruise and Sample

	Cruise 66-A-5 -- Microplankton samples (MP)											
	1	2	3	4	5	6	7	8	9	10	11	12
Depth (m)	10-0	100-0	0	0	100-0	10-0	0	10-0	100-0	0	10-0	100-0
Dinophysis balechi												
D. circumsuta												
D. doryphora	+		+		+		+		+		+	+
D. hastata		+	+		+							+
D. odiosa	+											
D. paulseni												+
D. pusilla					+					+		+
D. schuetti					+						+	+
D. swezyi												
D. uracantha												

	Cruise 67-A-5 -- Bongo-net samples (BN)												
	5	8	9	10	12	13	14	15	16	17	18	20	22
Depth (m)	0	25-30	55-65	110-120	0	25-30	55-65	110-120	226-112	635-400	750-650	0	0-64
Dinophysis balechi													
D. circumsuta								+					
D. doryphora		+	+	+		+	+		+				+
D. hastata			+		+			+				+	+
D. odiosa													
D. paulseni			+	+					+				
D. pusilla			+			+			+				+
D. schuetti			+			+	+	+	+				
D. swezyi								+					
D. uracantha				?				+	+				

	Cruise 68-A-4 -- Pump samples (P)											
	1	2A	2B	2C-G	14ACEGIK	14BDFHJL	15A	15B	16B	16C	17A	17B
Depth (m)	10	15	15	0-10	15	0-4	175	0-4	5-9	5-9	5-9	0-4
Dinophysis balechi					+	+				+		
D. circumsuta												
D. doryphora			+		+	+		+	+	+	+	+
D. hastata									+			
D. odiosa												
D. paulseni												
D. pusilla					+	+				+		+
D. schuetti					+	+				+	+	+
D. swezyi												
D. uracantha												

TABLE 2

Depth Ranges for Individual Species of *Dinophysis*

Depth (m) of samples	*D. balechi*	*D. circumsuta*	*D. doryphora*	*D. hastata*	*D. odiosa*	*D. paulseni*	*D. pusilla*	*D. schuetti*	*D. swezyi*	*D. uracantha*
0–4	+		+	+			+	+		
5–15	+		+	+	+		+	+		
25–30			+				+	+		
55–65			+	+		+	+	+		
110–120		+	+	+		+		+	+	+
226–112			+			+	+	+		+

genus *Dinophysis* as a whole may have 18 plates rather than 17 as indicated by Tai and Skogsberg.

The minuteness of this additional plate is a probable reason for its previous omission; its position, in the generally small epitheca, is another factor. In addition to being difficult to see, its small size provides little leverage by which mechanical stress can be an aid to separating it from other plates. Perhaps the most significant reason for it being overlooked is in the analysis technique. In this connection one necessarily must carry out dissection under oil immersion. Otherwise, this plate may be overlooked. Experience with individuals having a relatively small epitheca indicates that several applications of sodium hypochlorite, and patience are necessary to observe the separation of this plate.

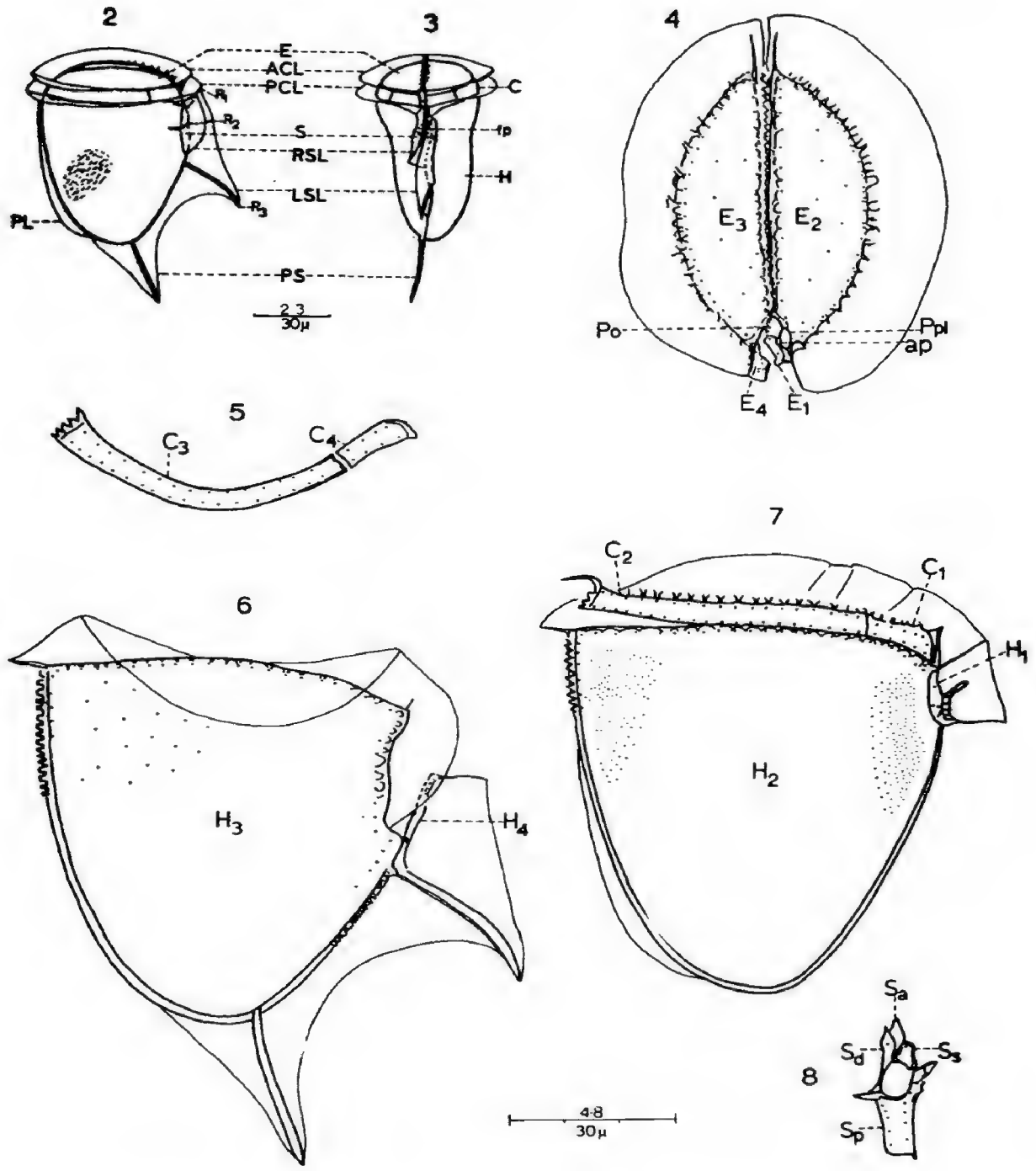
General Plate Pattern

The arrangement of the thecal plates of the Dinophysoidae was first established by Tai and Skogsberg (1934). They explain the position of individual plates relative to one another. This explanation has been repeated in various degrees, most recently by Balech (1967c) and Norris (1969). With the exception of the additional plate found, the general arrangement of plates in all species discussed here is the same as in previous works. The following is a general account of the thecal plates of *Dinophysis* including some details not previously noted (see Figs. 2–8).

The theca is composed of 18 plates; all previous works report 17. The epitheca is made up of six plates, the cingulum four, the hypotheca four, and the sulcus four.

The epithecal plates are: the left and right dorsal epithecal plates (E_2 and E_3), the left and right ventral epithecal plates (E_1 and E_4), the pore plate (Po), and the sixth epithecal plate, referred to here as the pore platelet (Ppl) and described for the first time. The latter plate receives its name because of the close relationship to the apical pore and its being generally smaller than the pore plate.

The two dorsal epithecal plates make up most of the epitheca. They are connected at a sagittal fission suture. Ventrally each dorsal plate has a small notch. The notch of the left plate (E_2) is somewhat larger and is filled by the left ventral epithecal plate (E_1), the pore plate (Po) and the pore platelet (Ppl). The notch



FIGS. 2–8. *Dinophysis circumsuta*. 2 and 3, right lateral and ventral views illustrating principal features; 4, apical view of epithecal plates starting to separate; 5, the two right cingular plates; 6, the two right hypothecal plates; 7, the two left cingular and the two left hypothecal plates as seen from within; 8, ventral view of the sulcal plates. (ACL, anterior cingular list; C, cingulum; C_1, left ventral cingular plate; C_2, left dorsal cingular plate; C_3, right dorsal cingular plate; C_4, right ventral cingular plate; E, epitheca; E_1, left ventral epithecal plate; E_2, left dorsal epithecal plate; E_3, right dorsal epithecal plate; E_4, right ventral epithecal plate; H, hypotheca; H_1, left ventral hypothecal plate; H_2, left dorsal hypothecal plate; H_3, right dorsal hypothecal plate; H_4, right ventral hypothecal plate; LSL, left sulcal list; PCL, posterior cingular list; PL, parasagittal list; Po, pore plate; Ppl, pore platelet; PS, posterior sail; R_1, anterior main rib; R_2 fission rib; R_3, posterior main rib; RSL, right sulcal list; S, sulcus, S_a, anterior sulcal plate; S_d, right (dextral) sulcal plate; S_p, posterior sulcal plate; S_s, left (sinistral) sulcal plate; ap, apical pore; fp, flagellar pore).

of the right plate (E_3) is occupied by the right ventral epithecal plate and sometimes in part by the left ventral epithecal plate and/or the pore plate. Each dorsal epithecal plate possesses a list (membrane) along its lateral edge. These lists make up the larger portion of the anterior cingular list.

The pore plate (Po) is quite small and lies in the ventral notch of E_2 and also connects with a small portion of E_3. It seems to lie always wholly or in part dorsal to the apical pore. In only one instance (*D. odiosa*) is a pore believed to be present in Po. This plate has a list in some individuals.

The pore platelet (Ppl) is typically smaller than Po and lies to the left and/or ventral to Po. It generally appears to make up the left margin of the apical pore. This plate is in contact with the left ventral epithecal plate, the left dorsal epithecal plate, and the pore plate. There is no pore in Ppl but it does have a list in some individuals. Near the middle of the margin of the ventral notch of E_2 there generally is a small denticle marking the suture between the pore plate and the pore platelet. The apical pore is located near the ventral edge of the epitheca and is enclosed by E_1, Po and Ppl.

The ventral epithecal plates are small but typically larger than Po. The left one (E_1) in some cases (if not all) touches the other five epithecal plates. It is situated ventral to Po and Ppl in the notch of E_2 and generally forms the ventral portion of the apical pore. The right one (E_4) is generally smaller and is in the ventral notch of E_3. Ventrally, these plates are inclined to meet two of the sulcal plates. Each ventral epithecal plate has a list, generally subrectangular, which connects with the list of its partner and with that of the corresponding dorsal epithecal plate. Generally, there is one pore in each plate.

The cingular plates are: the left and right dorsal cingular plates (C_2 and C_3) and the left and right ventral cingular plates (C_1 and C_4). They are arranged in an incomplete transverse ring. Dorsally, C_2 and C_3 are connected at the sagittal fission suture which is generally denticulated; ventrally, C_1 and C_4 are separated by the anterior and the right sulcal plates.

The dorsal cingular plates are considerably larger than the ventral ones. They are nearly mirror images of each other though the right one (C_3) tends to be slightly the larger. Lists are sometimes present. Two distinct rows of pores, one each near the anterior and posterior margins, are present on both plates.

The ventral cingular plates vary in size and shape. Typically, the left plate (C_1) is the larger. Both plates have one or more pores and occasionally have a list.

The hypothecal plates are: the left and right dorsal hypothecal plates (H_2 and H_3) and the left and right ventral hypothecal plates (H_1 and H_4).

The dorsal hypothecal plates are the largest plates of the theca and may dominate the shape of the body. In the left one (H_2) there is a notch at the ventro-anterior corner, into which the left ventral hypothecal plate (H_1) fits. The right plate (H_3) has a wider and longer notch extending farther posteriorly than that of H_2; this notch is occupied by the right ventral hypothecal plate (H_4) and the right and posterior sulcal plates. The dorsal hypothecal plates are joined together at the sagittal fission suture extending from the cingulum on the dorsal side to the ventral notch of H_3; anterior to this point, their ventral margins are separated

by the left and right ventral hypothecal plates and the sulcal plates. Each dorsal hypothecal plate possesses a membranous list along its anterior edge. These lists make up the posterior cingular list and they meet on the dorsal side. Ventrally, the list on H_2 is attached to the anterior edge of the list of H_1. The list on H_3 continues posteriorly as the right sulcal list along the ventral margin to a point near the end of the sulcus. H_3 also possesses a comparatively small list behind the posterior main rib (R_3) of the left sulcal list, it is a continuation of the left sulcal list. In addition, all members in the "hastata" group have another list on H_3 which is situated posteriorly and is often called the posterior sail (PS). In some instances, the posterior sail is continuous with the left sulcal list. Both dorsal hypothecal plates generally have some structural differentiation. They always have minute to small scattered pores and also pores arranged in a row near the perimeter.

The ventral hypothecal plates (H_1 and H_4) are narrow, elongated plates. Since they are usually seen from the side they are most readily recognized by their lists. The left plate (H_1) is embedded in the ventroanterior notch of H_2 to which its left margin is attached. Its right lateral margin connects with the anterior portion of the posterior sulcal plate and also with the left sulcal plate. The right plate (H_4) is generally somewhat longer than H_1 and rests in the notch of H_3, almost immediately behind H_1. Its left margin connects to H_2 at the sagittal fission suture. Most of the right margin is attached to the posterior sulcal plate, the remainder to H_3. The list of the left plate (H_1) is the anterior portion of the left sulcal list, the list of the right plate (H_4) is the posterior portion. The left sulcal list typically has three main ribs: the anterior main rib (R_1), the fission rib (R_2) and the posterior main rib (R_3).

The sulcal plates are: the anterior plate (S_a), the left (sinistral) sulcal plate (S_s), the right (dextral) sulcal plate (S_d) and the posterior sulcal plate (S_p). Lists are occasionaly present on one or more sulcal plates; however, they are very small and seem to be more prevalent than indicated by previous writers. All four sulcal plates possess an inward directed process which, though sometimes reduced, is always present. The sulcus extends from near the anterior region of the cingulum, where S_a and S_d meet E_1 and E_4, to some distance down the right side of H_4.

The anterior sulcal plate (S_a) is narrow, elongate and possesses an inward directed process near the posterior end. Anteriorly, this plate nearly always touches both E_1 and E_4. Laterally, it touches C_1 and S_s to the left and S_d to the right. Its posterior end borders the flagellar pore. This plate was never seen to possess a list or a pore.

The left sulcal plate (S_s) is the smallest of the sulcal plates. It frames the left anterior portion of the flagellar pore, is somewhat comma-shaped, and has a right anterior or right medial inward directed process. This process appears to run confluent with that of S_a. S_s touches C_1 anteriorly, H_1 to the left, S_a to the right and S_p posteriorly. In one instance, S_s had a small narrow list. It has one pore in some species.

The right sulcal plate (S_d) is generally somewhat larger than S_a and smaller than S_p. It forms the right anterior portion of the flagellar pore. Its narrow pos-

terior extension has an inward directed process. This plate appears always to abut E_4 anteriorly, S_a to the left, C_4 and H_3 to the right and S_p posteriorly. It is most apt of the sulcal plates to possess a list. One or two pores may be present.

The posterior sulcal plate (S_p) is the largest of the sulcal series. Generally, it forms the posterior half of the flagellar pore; sometimes a little more on the left and less on the right. Its anterior margin is always concaved to accommodate the flagellar pore. The right apophysis has an inward directed process which runs confluent with that of S_d. S_p is attached to H_1 and H_4 to the left and H_3 to the right and posteriorly. A list rarely may be present and pores are present.

Dinophysis balechi, n. sp.

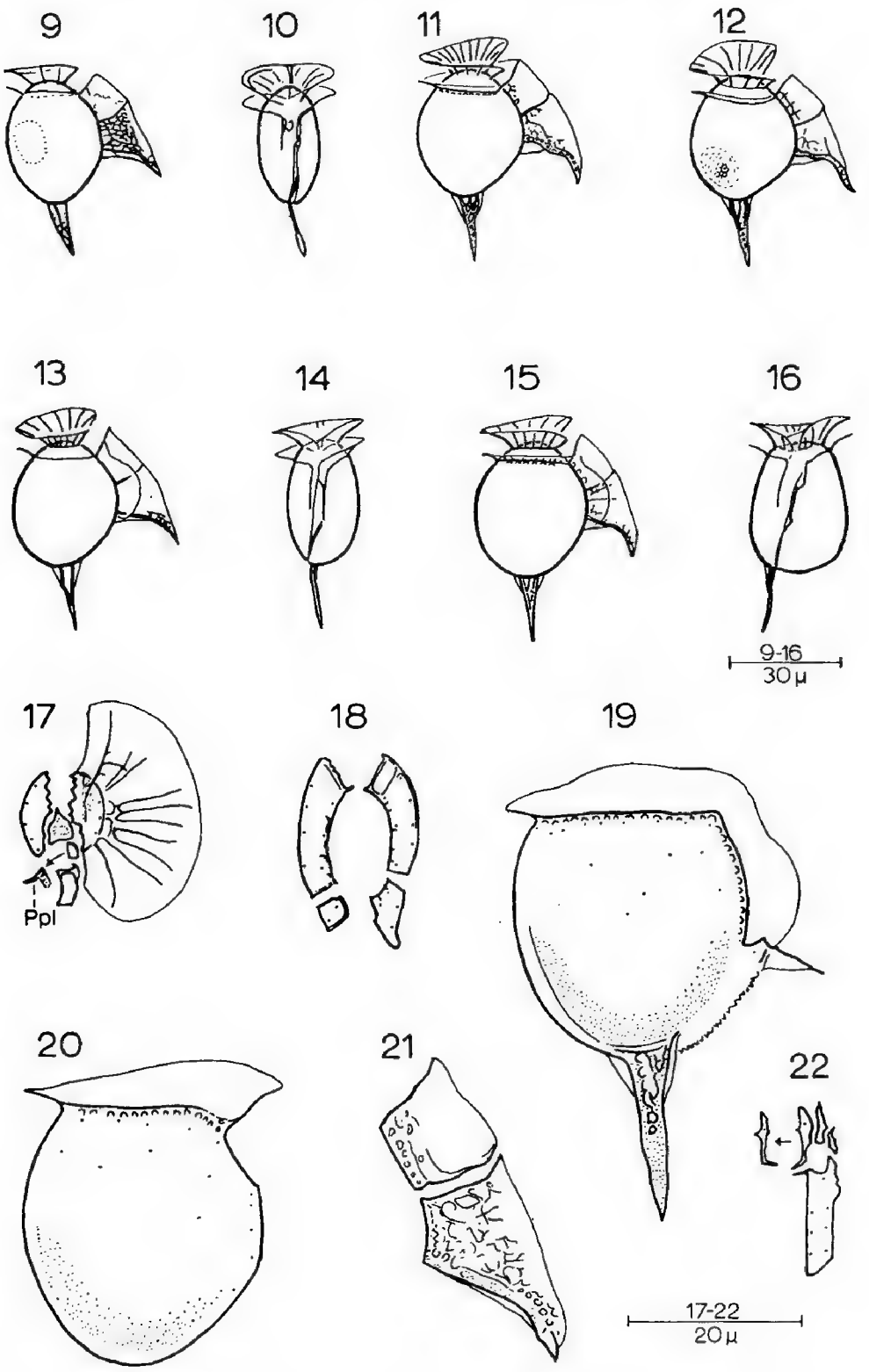
Figures 9–22

General

This is a rather small species. The body is irregularly elliptical in lateral view, rounded and asymmetrically tapered anteriorly and posteriorly and deepest near the middle. The length to depth ratio is 1.08–1.18:1. The longitudinal axis coincides (or nearly so) with the midline.

The epitheca is 0.28–0.37 as deep as the hypotheca, quite convexed, highest near the middle and well below the distal margin of the anterior cingular list. The cingulum is slightly convexed, its width is 1.75–2.33 the height of the epitheca. It is subuniform in width throughout its dorsoventral length. The posterior cingular list is 0.12–0.16 the body length from the apex. The hypotheca is somewhat asymmetrical. The dosal margin is moderately and fairly uniformly convexed. The ventral margin is somewhat more convexed and tends to be slightly flattened anteriorly and posteriorly. The posterior end is somewhat narrowly rounded, much as is the anterior though it may be slightly more or less so. In ventral view the body is narrowly subelliptical with rather symmetrical sides, and widest near the middle. The anterior and posterior ends are rather equally and uniformly rounded. The posterior end broadens more to make the body of megacytic individuals subovate in ventral view. The length to width ratio is 1.69–2.00:1 (1.38:1 in the megacytic individual); the depth of the cingulum to the transdiameter is 1.17–1.33:1 (1.09:1 in the megacytic individual).

The anterior cingular list is 2.25–2.86 the width of the cingulum; the posterior is 0.44–0.55 the width of the anterior. Both lists are inclined anteriorly, the first 26°, the latter 11–24°. The anterior is rather funnel-shaped. Simple, nearly complete and weak radial ribs are present in irregular number and distribution on the anterior list while the posterior list is smooth. One individual had a submarginal rib connecting the radial ribs on the right list only. The left sulcal list is 0.55–0.56 the body length and widest at R_3. The distal margin of the anterior portion is rather straight and oblique, forming an angle of 43–52° with the midline. Between R_2 and R_3, this margin is not so oblique but straight or partially so with an irregular convexity. The posterior margin is slightly concaved or sigmoid. A moderately to strongly acute angle is formed at R_3. R_2 is 0.32–0.35, R_3 0.64–0.72



FIGS. 9–22. *Dinophysis balechi*, n. sp. 9 and 10, an individual from sample P-16C; 11 and 12, two individuals from P-16C; 13 and 14, an individual from sample P-14L; 15 and 16, a megacytic specimen from sample P-14E; 10, 14, and 16 are in ventral view, the others in right lateral view. 17–22, plates from individual illustrated in Fig. 11: 17, epithecal plates with omission of E_4 and the list of E_3; 18, the cingular plates; 19, H_3; 20, H_2 from within; 21, H_1 and H_4; 22, the sulcal plates with S_d shown in two views.

the greatest body depth. The ribs of this list are weak to fairly well developed. R_1 is straight to slightly sigmoid; R_2 is gently to moderately concaved forward. R_3 is rather straight or sigmoid proximally and then it has a moderate to strong posterior concavity. It is inclined 24–38° posteriorly. The left sulcal list may be

smooth but more developed individuals have irregular ribbing—to the extent of reticulation, especially between R_2 and R_3. The right sulcal list (seen with the aid of trypan blue) ends near R_3, though the free margin may extend posterior to this rib. It is unique compared to that of other species, narrow anteriorly and then broader and uniformly and moderately convexed over the larger posterior portion. This list is smooth and tenuous. The posterior sail is on or near the midline and is inclined 6–16.5° ventrally. It is narrow and elongate, being ca. 0.36–0.47 as wide at the base as it is long. There are two main ribs, they may have some anastomoses between them and are fused to one distally; or there may be just one main medial rib. The ribs are of moderate strength and are typically bordered proximally by a small narrow list. When the medial rib is present, the margins of the list are thickened and extend the length of the rib and form anastomoses with it distally. The length of the posterior sail is 0.54–0.67 the body depth.

Thecal Plates

The thecal wall is thin and may become indistinct with application of sodium hypochlorite, this can be most disconcerting during plate analysis. The small epitheca is irregularly ellipsoidal in apical view, the right half being somewhat longer (dorsoventrally) than the left. Each dorsal plate has irregular, small to medium, rounded to pointed denticles along the sagittal suture. The ventral notch in each plate is relatively large, especially in E_3 which may be confused with E_2 when separated. These plates are smooth and each has a row of pores near the lateral margin. There is a parasagittal list present on E_2. Its appearance is more like a thick ridge than a list and it appears to continue up the anterior cingular list. The small, ventral epithecal plates are comparatively thick; the presence of pores was not confirmed.

The pore plate is relatively thick and subrectangular. Its shape may be masked by the presence of a comparatively large, thick list, a continuation of the parasagittal list of E_2. This list is as much as 2 μ above the cell wall which is its greatest height except for a possible continuation along the anterior cingular list.

The pore platelet is smaller than the pore plate, subtrapezoidal and thick. It appears to border the left ventral portion of the apical pore. There is also a list on this platelet, a continuation of the parasagittal list. This platelet touches E_1 ventrally and to the right, E_2 to the left and some ventrally and Po dorsally. This interpretation of the arrangement may be modified by further study of the small and delicate epitheca of additional specimens. Phase-contrast microscopy would be helpful in such a study. The apical pore seems to be enclosed by Po, Ppl and E_1. In fact, it may be closed completely or at least hidden by the thickened parasagittal list on Po and Ppl.

The cingular plates are smooth. C_1 is 1.68–2.65 C_4; it broadens ventrally, especially posteroventrally where it ends in a denticle or finger-like projection. C_4 is subrectangular, nearly square. The dorsal plates have three pores near the anterior border and four near the posterior. C_1 has one or two pores near the

anterior and two near the posterior; C_4 has one near each of these two margins.

The dorsal hypothecal plates have rather small and rounded denticles along the sagittal suture. The anteroventral notch in H_3 is distinctive. In addition to its relative greater length, the right margin of this notch extends slightly beyond the sagittal margin near R_3 thus making the posterior margin oblique in the reverse direction from that of any species in the "hastata" group which has been dissected. Closely knit, small, tenuous poroids are present in both plates. The ventral hypothecal plates together are ca. 0.51–0.56 the length of the hypotheca. H_1 tends to be slightly longer than H_4. This is a more obvious difference from most species of *Dinophysis*; *i.e.*, typically H_4 is the larger (Tai and Skogsberg 1934: 395); subequal to, or a little longer than H_1 (Abé 1967a: 378). This characteristic was observed to be true in all the individuals examined. H_4 is 0.83–0.97 the length of H_1. Each ventral hypothecal plate is believed to have three or four pores.

The sulcus is ca. 1.14–1.36 the length of H_1 and H_4 together. This too is unusual as typically the ventral hypothecal plates are subequal to or a little longer than the sulcus (Abé 1967a: 378). The sulcus extends to the posterior end of H_4. The anterior sulcal plate is narrow and elongate and may be somewhat sigmoid shaped. The left sulcal plate has no pore.

The right sulcal plate is slightly longer than S_a but only 0.42–0.53 length of S_p. The left margin is slightly sigmoid, the right is concaved anteriorly and posteriorly where it touches C_4 and H_3 respectively. There is a hint of a list on the right side. One pore is present.

The posterior sulcal plate (S_p) is elongated, 1.53–1.89 the length of H_4 and 0.33–0.38 the body length. S_p is relatively longer in this species than in all the others examined. The left margin may be without distinct denticles or it may have small, irregular ones on the anterior ⅓. Except for the possible denticles on the left, both lateral margins are quite straight and parallel. The posterior margin is oblique, from the left margin posteriorly to the right. This is unique among the species examined and gives the characteristic indentation to the anteroventral notch of H_3 mentioned above. There are four to five pores near the left margin and two to three near the right.

The nucleus is ellipsoidal, somewhat elongated, and located dorsally and perhaps somewhat posteriorly. In one instance it possessed a distinct polygonal network throughout. One individual retained a brownish-yellow color throughout the rather homogeneous protoplasm, even after dissection. There were no distinct inclusions save possible scattered oil droplets.

Dimensions

Body length, 32.5–34; total length, 47–52; epithecal depth, 8–10; hypothecal depth, 26–28.5; transdiameter, 13–15; body width, 16.5–19.5; maximum width of the left sulcal list, 14–18; R_1–R_2 8.5–9(10–12); R_2–R_3 7–7.5(22.5–26); R_3–PS 20–21.5(31.5–37).

Four specimens (plus one megacytic individual) were measured and four examined for their plate morphology.

Variations

On the whole, the individuals examined are quite similar. More obvious variations are: the number of ribs in the anterior cingular list, the shape of R_3, the degree of reticulation in the left sulcal list, the structure of the posterior sail and the presence of an extra cingular plate. The latter was observed once, occurring between C_1 and C_2. Constant characters include the relative size of H_1 versus H_4, the oblique (from left to right) posterior margin of S_p and the uniquely shaped right sulcal list. The latter characteristic is unique to this species as far as is known.

Dinophysis balechi is closely related to *D. hastata*, *D. alata*, and *D. pusilla*. *D. balechi* differs from *D. hastata* and *D. alata* in having a relatively smaller epitheca and a larger right sulcal list. The relative length of H_1 versus H_4 and the shape and relative length of the posterior sulcal plate also separate *D. balechi* from *D. hastata*, as defined in this paper. Further separation from *D. alata* is indicated by the different shapes of their left sulcal lists and in that *D. balechi* lacks the parasagittal list present on the dorsal side of *D. alata*.

D. pusilla is more rotund than *D. balechi*, lacks ribs in the anterior cingular list and has a much smaller right sulcal list. The relative length of H_1 versus H_4 and the relative length and shape of the posterior sulcal plate are further evidence of their separation.

The specific name is in honor of Professor Enrique Balech.

Dinophysis circumsuta (Karsten) Balech

Figures 2–8

Phalacroma circumsutum Karsten 1907: 421, pl. 53, fig. 8.—Kofoid and Skogsberg 1928: 182, fig. 23:6—Silva 1958: 20, pl. 1, fig. 3.—Wood 1963: 5, fig. 6.
Phalacroma doryphorum (Stein) Halim 1960: pl. 1, fig. 27.
Dinophysis circumsutum (Karsten) Balech 1967c: 82.

General

The body of the medium-sized individual representing this species is subobovate in lateral view, gently rounded anteriorly, asymmetrically tapered posteriorly, and deepest somewhat anterior to the middle. The length to depth ratio is 1.30:1. The longitudinal axis coinsides with or is slightly ventral to the midline.

The epitheca is 0.84 as deep as the hypotheca, symmetrical, gently to moderately convexed, highest near the middle, and visible above the anterior cingular list. The cingulum is flat to slightly convexed; its width is equal to the height of the epitheca and is subuniform throughout its dorsoventral length. The posterior cingular list is 0.15 the body length from the apex. The hypotheca is asymmetrical. The dorsal margin is gently convexed to nearly flat. The ventral margin is nearly flat anteriorly, with a broad curve between R_2 and R_3 and rather flat posteriorly. The posterior end is asymmetrically tapered and considerably narrower than the anterior. In ventral view the body is spatulate, constricted anterior to

the middle, with rather symmetrical sides, and widest just behind the posterior cingular list. This shape is unique among the species examined. The posterior end is narrowly rounded compared to the anterior. The length to width ratio is 1.76:1, the depth of the cingulum to the transdiameter is is 1.29:1.

The anterior cingular list is 1.50 the width of the cingulum; the posterior is 0.89 the width of the anterior. Their anterior inclinations are 11° and 7° respectively. Both lists are smooth though they have short basal ribs. The left sulcal list to the base of R_3 is 0.34 the body length and ca. 2.70 wider at R_3 than anteriorly. The ventral margin is oblique and gently sigmoid. Behind R_3 the free margin has a strong concavity and is continuous with the posterior sail. It forms an angle of ca. 40° at R_3. R_2 is 0.21, R_3 0.53 the greatest body depth. The ribs of this list are weak to well developed. R_1 and R_2 are nearly straight; R_3 has a gentle posterior concavity and is inclined posteriorly 36°. The left sulcal list is smooth except for some structural differentiation in front of R_2. The right sulcal list ends somewhat in front of R_3; it is subuniform in width over the anterior half, tapers posteriorly and is smooth. The rather large posterior sail is continuous with the left sulcal list. It is largely ventral to the midline and is inclined ventrally. The inclination of the well developed central rib is 27°. The margins are smooth, the ventral is rather straight distally and then confluent with the left sulcal list, the dorsal margin is gently sigmoid. The length of this list at the center spine is 0.47 the body depth. There is a narrow parasagittal list along the dorsal side of H_2. It extends from the posterior cingular list posteriorly to near the antapex and is not confluent with the posterior sail. It is broadest dorsoposteriorly and its widest point is subequal to or slightly narrower than the width of the cingulum. The parasagittal list is smooth.

Thecal Plates

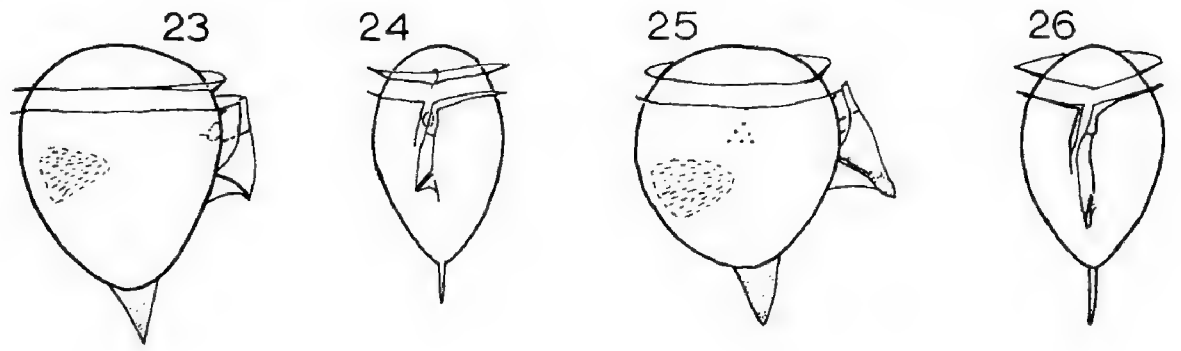
The thecal wall is comparatively thick and strong. The epitheca is subelliptical in apical view. The dorsal epithecal plates have comparatively small, pointed denticles along the sagittal suture. Both plates are smooth over most of their area, each has a row of pores near the perimeter and a few scattered pores. There is a parasagittal ridge near the suture line on each plate; in addition, there is a very narrow list on the ridge of E_2 which is absent from E_3. In apical view, the ventral epithecal plates appear to be elongated. E_1 forms the ventral and right margins of the apical pore and has two pores itself E_4 has one pore.

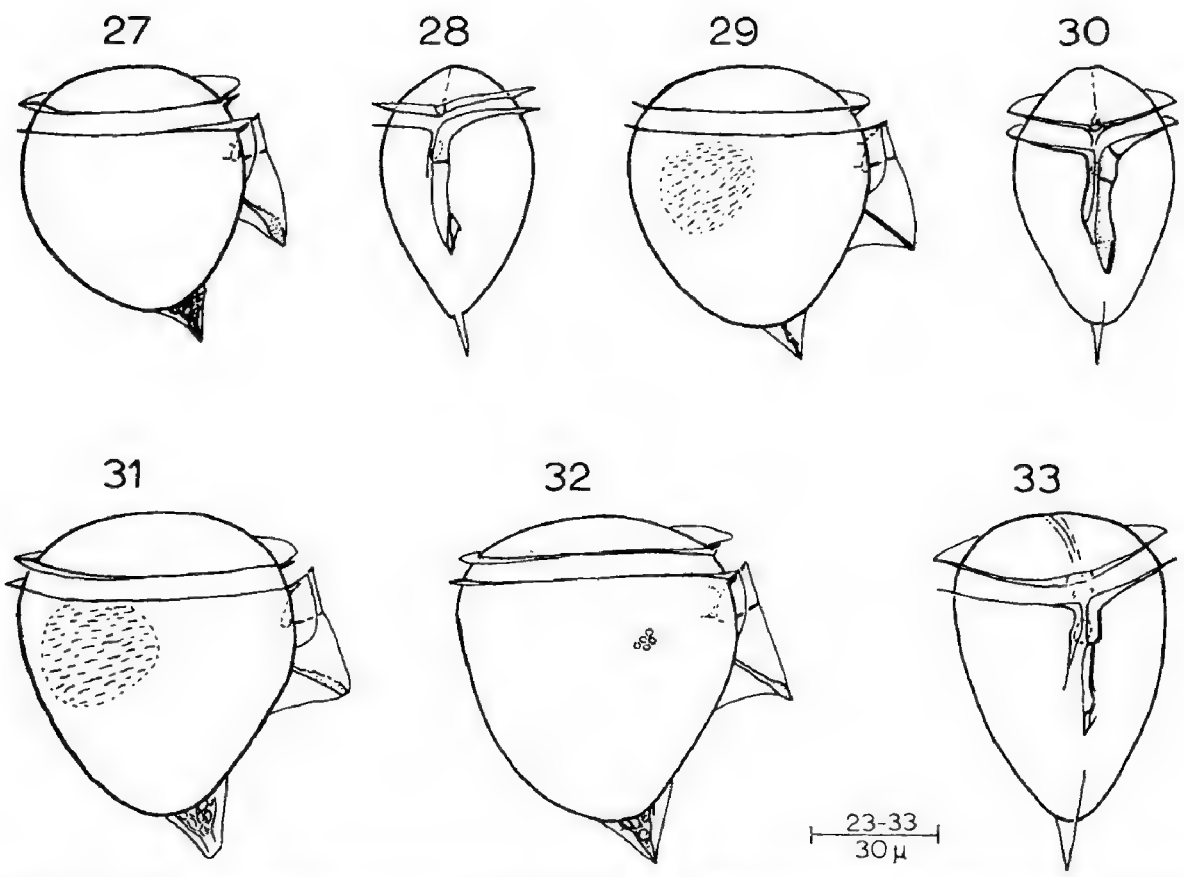
The pore plate is subrectangular to trapeziform, it forms the dorsal margin of the apical pore. The pore platelet is smaller than the pore plate and it is a truncated-cresent shape. It forms the left margin of the apical pore. Ppl touches E_1 ventrally, E_2 to the left and dorsally and Po to the right.

The cingular plates are smooth. The ventral plates are subrectangular and subequal in length, C_1 tending to be slightly longer. There appears to be a list along the anterior margin of all four plates; these lists are apparently confluent with the anterior cingular list *in situ*. There is also a narrow list along the ventral margin of each ventral plate. All four cingular plates possess a row of pores near both the anterior and posterior margins.

The dorsal hypothecal plates have comparatively small but distinct, irregular, truncated to pointed denticles along the sagittal suture. Closely spaced, moderately prominent poroids are present on both plates. The ventral hypothecal plates together are 0.41 the length of the hypotheca. H_4 is 1.74 the length of H_1. H_1 has three pores, H_4 has eight in a row.

The sulcus is slightly shorter than H_1 and H_4 together. It extends from just anterior to H_1 to 0.65 of the way down H_4. The anterior sulcal plate is 0.46 the length of S_p. Having a narrow posterior portion, it appears similar to S_d. The right margin is slightly sigmoid. The left sulcal plate (S_s) is the shortest in the group, it appears however, to be wider than either S_a or S_d. It is somewhat comma-shaped though the posterior portion is slightly abbreviated. There is a short outward directed process posteriorly. One pore is present. The right sulcal plate (S_d) is 1.50 the length of S_a and 0.69 the length of S_p. It forms most of the right and the right anterior portion of the flagellar pore. One pore is present.





FIGS. 23–33. *Dinophysis doryphora*. 23 and 24, two specimens from sample BN-10; 25 and 26, an individual from sample BN-13; 27 and 28, an individual from sample BN-9; 29 and 30, an individual from sample BN-22; 31, an individual from BN-9; 32 and 33, an individual from BN-14, 24, 26, 28, 30, and 33 are in ventral view, the others are in right lateral view.

The posterior sulcal plate (S_p) is slightly shorter than H_4, and 0.23 the body length. It frames most of the left, the posterior and part of the right posterior portion of the flagellar pore. The left apophysis is comparatively long and also has an outward directed process which is confluent with the shorter process of S_s. Associated with this process is a small triangular list which extends to the left margin of the flagellar pore. Along the outer margin of the left apophysis are three or four distinct denticles. Behind the anterior apophyses, the lateral margins are subparallel, the posterior is truncate with a distinct denticle at the left posterior corner. There are five pores near the left margin, one of which is in the large apophysis and five pores near the right margin.

The nucleus is relatively small, subellipsoidal, and located mostly in the dorsoposterior quadrant of the cell.

Dimensions

Body length, 74; total length, 94; epithecal depth, 48; hypothetical depth, 57; transdiameter, 41; body width, 42; maximum width of left sulcal list, 27; R_1–R_2 10(14.5); R_2–R_3 16(36); R_3–PS 37(51).

The only available specimen was measured and examined for its plate morphology.

Dinophysis circumsuta is separated from its closest relative, *D. doryphora*, by having the left sulcal list continuous with the posterior sail and by not having a club-shaped R_3 (see Kofoid and Skogsberg, 1928: 185). In addition, *D. circumsuta* is spatulate in ventral view and has a well developed medial rib in the posterior sail. The outline in ventral view has not been reported previously; otherwise, the individual representing *D. circumsuta* in this study is rather similar to those of previous reports.

Dinophysis doryphora (Stein) Abé
Figures 23–45

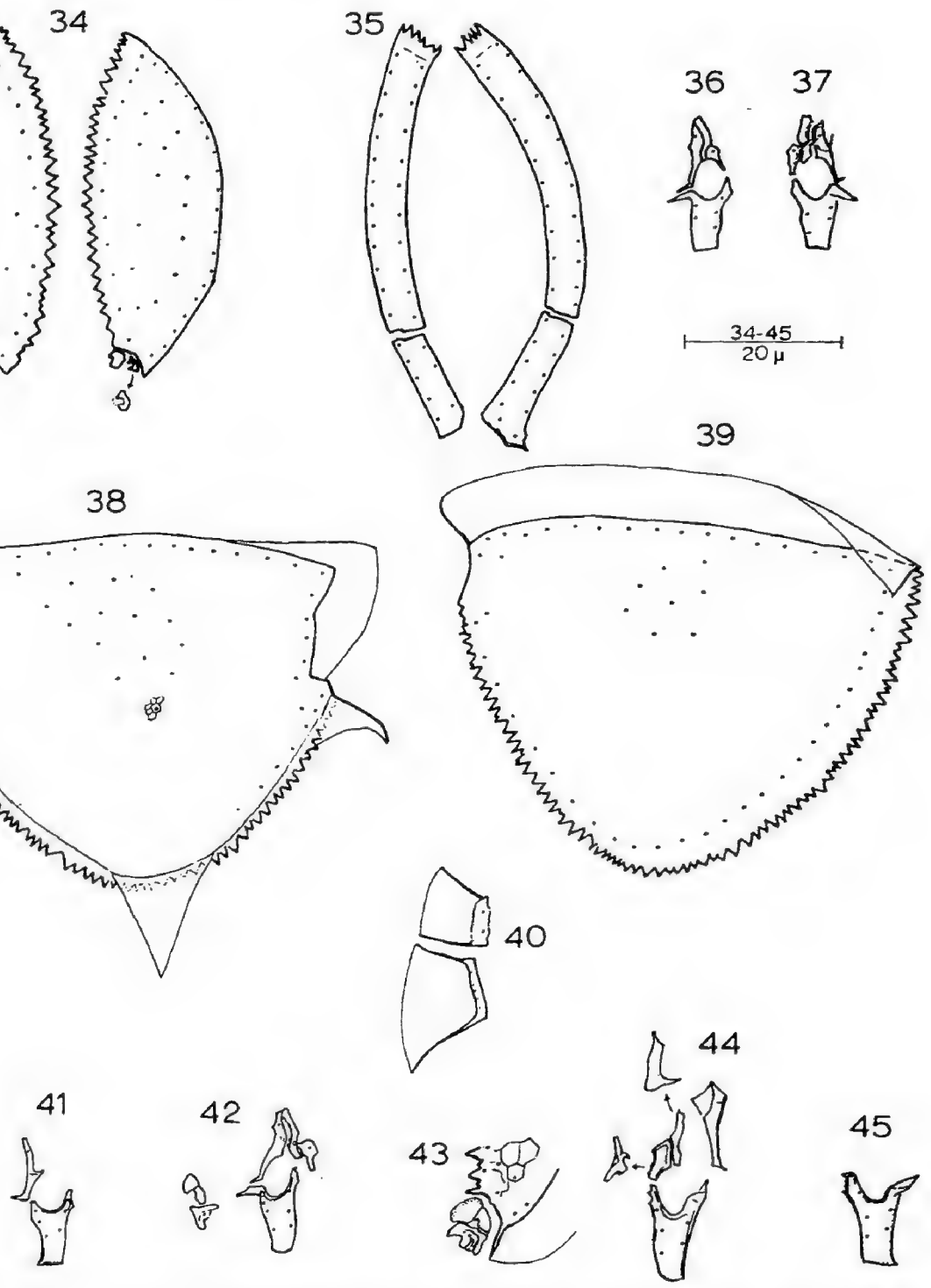
Phalacroma doryphorum Stein 1883: 23, pl. 19, figs. 1–4.—Kofoid and Skogsberg 1928: 175, fig. 23:1–5.—Rampi 1940: 257, fig. 27.—Wood 1954: 191, fig. 30.

Dinophysis doryphorum (Stein) Abé 1967b: 77, fig. 26.—Balech 1967c: 82.

General

The body of this medium sized species is subobovate in lateral view, rounded to broadly arched anteriorly, asymmetrically tapered posteriorly and deepest in the anterior half or near the middle. The length to depth ratio is 1.08–1.18:1. The longitudinal axis is deflected 0–4.5° ventrally.

The epitheca is 0.75–0.88 as deep as the hypotheca, moderately convexed to well rounded, highest near the middle and easily visible above the anterior cingular list. The cingulum is slightly convex or rarely flat; its width is 0.40–0.71 the height of the epitheca. It is subuniform in width throughout its dorsoventral length. The posterior cingular list is ca. 0.21–0.28 the body length from the apex. The hypotheca is rather variable and nearly symmetrical to somewhat asym-



FIGS. 34–45. Thecal plates of *Dinophysis doryphora*. 34, epithecal plates showing E_2, E_3, Po, and Ppl with the anterior cingular list omitted; 35, cingular plates; 36, sulcal plates from individual similar to one illustrated in Figs. 25 and 26; 37, sulcal plates as seen from within; 38–40, hypothecal plates; 41, S_d and S_p from individual similar to one illustrated in Fig. 23; 42, Po, Ppl, E_1, and the sulcal plates from individual illustrated in Figs. 27 and 28; 43, ventral region of E_2 with Po, Ppl, and E_1; 44, sulcal plates as seen from within and showing S_a and S_s in two views; 45, S_p as seen from within, from individual illustrated in Figs. 32 and 33. 34, 35, 37–40 are from individual illustrated in Fig. 23. 43 and 44 are from an individual similar to the one illustrated in Figs. 32 and 33.

metrical. The dorsal margin is moderately convexed to somewhat flattened. The ventral margin tends to be less convexed and more asymmetrical, sometimes being rather flat anteriorly and/or posteriorly. The posterior end is narrowly to moderately rounded with a varying degree of taper. It tends to be deeper in megacytic individuals. In ventral view the body is typically narrowly subobovate with rather symmetrical sides, widest near or anteriorly to the middle. The pos-

terior end is narrowly rounded compared to the anterior, it broadens to make the body subelliptical in advanced megacytic stages. The length to width ratio is 1.41–1.69:1 (1.27–1.46:1 in megacytic individuals); the depth of the cingulum to the transdiameter is 1.30–1.61:1 (1.20–1.27:1 in megacytic individuals).

Except in two of the nine individuals examined, the anterior cingular list is as wide or wider than the cingulum; the posterior is 0.33–0.67 the width of the anterior. Though occasionally inclined a little posteriorly, these lists are usually inclined anteriorly, as much as 27° (0.5–27°); there is a tendency for them to be more inclined ventrally and for the posterior list to be the more inclined of the two. Both cingular lists are smooth though they may have a hint of rib formation at their bases. The left sulcal list is 0.36–0.46 the body length and distinctly widest posteriorly. Its ventral margin is nearly straight, slightly sigmoid, irregular or convex. The posterior margin is gently to moderately concave. The free margin forms an angle of ca.53–83° at R_3. R_2 is 0.09–0.17, R_3 0.20–0.34 the greatest body depth. The ribs of this list are weak or of moderate strength. R_1 and R_2 are typically straight to moderately concave anteriorly; R_3 is straight to moderately concave posteriorly, may be weakly to strongly clubbed and is inclined posteriorly 22–48.5°. The left sulcal list is smooth except in two individuals observed which have weak markings in the anteroproximal 2/3. The right sulcal list (not always seen *in situ*) ends near R_3 but may appear to end about half way between R_2 and R_3; it is subuniform in width, rounded or gently tapering posteriorly. Weak ribs or markings are rarely observed in this list. Posteriorly there is an acute, triangular list which is situated on or somewhat ventrally to the midline and is inclined 3–27° ventrally. It is as wide at the base as it is long but may be slightly wider or narrower. This list is smooth and delicate, but may have some delicate structure, thickening reticulation, reticulation ending in a spine or it has a thickening at the apex which sometimes extends along the margins. The length of this list to the body depth ratio is 0.18–0.32:1.

Thecal Plates

The dorsal epithecal plates have small, rounded to comparatively large, pointed denticles along the zigzag sagittal fission suture. These plates are smooth or have a relatively large irregular polygonal reticulation. When present, this reticulation is always larger and more irregular than that on the hypotheca. Pores are arranged in a row near the perimeter and scattered over the remainder of each plate.

The pore plate (Po) is relatively thick and in different individuals and orientations appears to be subelliptical, trapeziform, rhomboidal or somewhat like a gnomon. The latter is due to denticles which connect with a small portion of the sagittal suture of E_3.

The pore platelet (Ppl) is relatively thick and subtriangular, rectangular or trapeziform. In one instance, two small spine-like projections were observed on this plate. It is surmised that they either project inward as "anchors" or are part of an indistinct list. The pore platelet borders the left and possibly part of the ventral and dorsal margins of the apical pore.

The cingular plates are generally quite smooth though they may be partially marked with incomplete reticulation. The ventral plates are subrectangular and subequal in length, C_1 tending to be slightly longer. C_1 is the most distinctive; it broadens ventrally, especially posteroventrally where it ends in a denticle of varying size. All four cingular plates possess a row of pores near the anterior and posterior margins.

The dorsal hypothecal plates have small, rounded to comparatively large, pointed denticles along the sagittal suture. These plates have a fine to moderate seized, irregular polygonal reticulation. This reticulation fades toward the margins, especially posteriorly where it was not observed. Unless observed under oil immersion, this reticulation may appear as closely knit poroids. The ventral hypothecal plates (H_1 and H_4) together are about 0.32–0.41 the length of the hypotheca. H_4 is ca. 1.25–2.00 the length of H_1 and possesses three pores in a row; H_1 has two pores.

The sulcus is subequal in length to H_1 and H_4 together. It extends to near the posterior end of H_4. The anterior plate (S_a) is subequal in length to H_1. This narrow elongated plate has a bend to the right in the posterior 0.3–0.5. The right sulcal plate (S_d) in at least some individuals has an outward directed rib at the base of the posterior extension. This may help support a small list along the right margin of S_d. One pore is present in S_d.

The posterior salcal plate (S_p) is subequal in length to H_4 and is 0.16–0.21 the body length. The left apophysis is the longer and may bear denticles on its left margin. Posteriorly to the anterior apophyses the left margin tends to be slightly convex, the right concave and the posterior truncate. There are two to three pores near both lateral margins.

The nucleus is oviform and in the dorsomedian region of the body. A few oil droplets may be seen scattered throughout the cell. In one instance highly reflective, dense particles were observed within a posteromedian vacuole.

Dimensions

Body length, 51–72; total length, 62–85; epithecal depth, 36–58; hypothecal depth, 44–66; transdiameter, 27–44; body width, 31–48; maximum width of the left sulcal list, 9–16; R_1–R_2 4.5–8(7.5–10); R_2–R_3 8–12(16–27); R_3–PS 28.5–41(30–49).

Seventeen specimens (plus six megacytic individuals) were measured and nine (plus two) examined for their plate morphology.

Variations

The specimens examined exhibit considerable variability. Based on body size and shape, the angle of the posterior sail, and the shape of the left sulcal plate they can be placed in three general groups. The first form (Figs. 23–26) has a length of 51—57.5 μ and the posterior sail is always inclined less than 10° ventrally. The second group (Figs. 27–30) has a length of 59–62 μ and the posterior sail is always inclined more than 15°. The body shapes and left sulcal plates of these two forms agree quite well. Though the third form (Figs. 31–33) agrees

with the second in regards to the posterior sail, it is unique in the other aspects. Its length is consistently greater than 70 μ, its general shape distinct, and its left sulcal plate seems to be somewhat irregular. There is some doubt about the latter character because only two non-megacytic individuals were dissected. This form has its deepest and widest point somewhat more anteriorly than the others.

The variations of the specimens found in this study are similar to those shown in earlier works. Though the plate analyses reveal variations, there is not sufficient evidence to justify "splitting" this species on the basis of plate morphology.

Dinophysis doryphora differs from its closest relative, *D. circumsuta*, in having the left sulcal list and the posterior sail separated and in that R_3 generally is club-shaped (see Kofoid and Skogsberg 1928: 178). Furthermore, *D. doryphora* does not have a well developed solid spine in the posterior sail and its outline in ventral view is subobovate, not spatulate.

Dinophysis hastata Stein
Figures 46–59

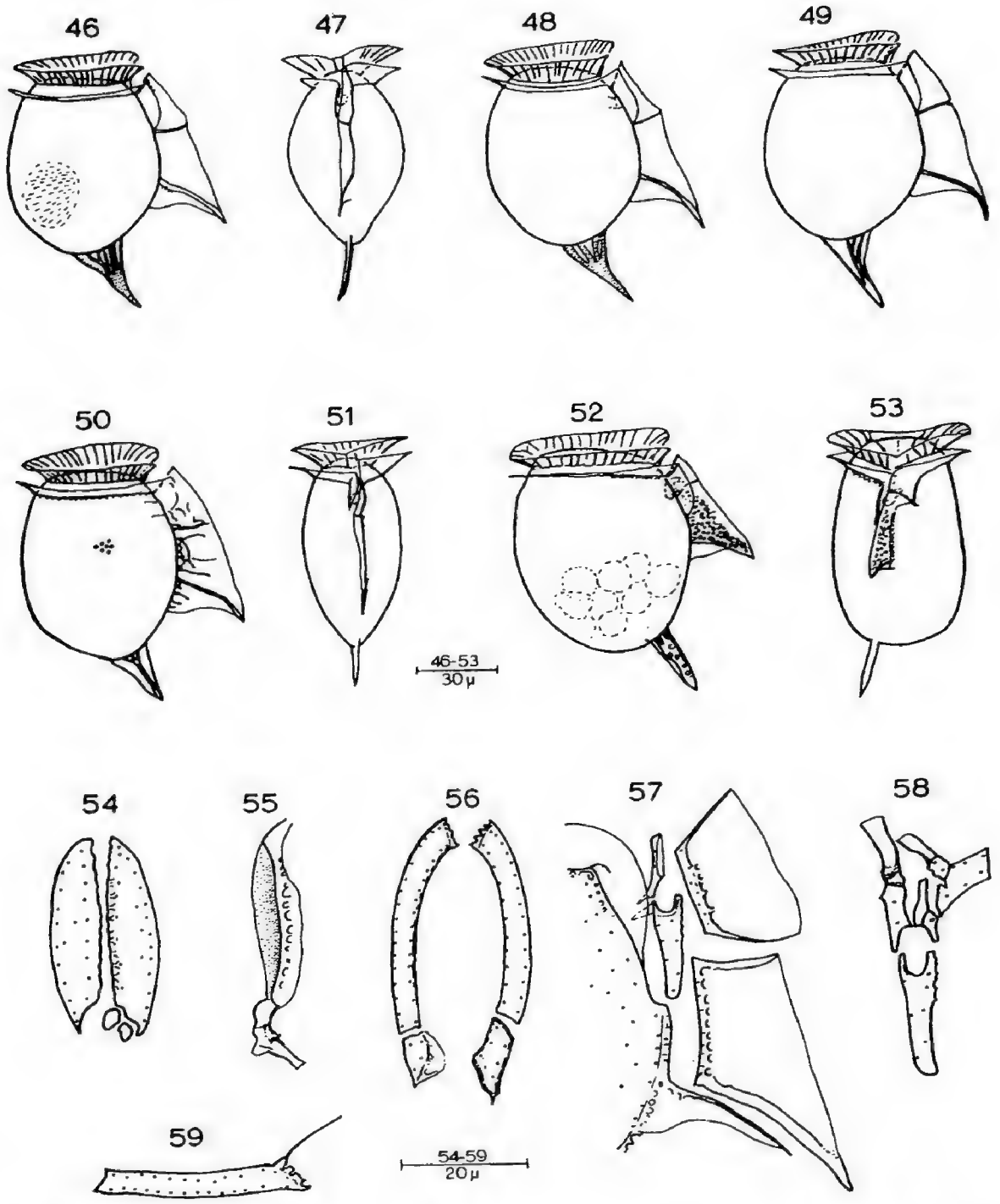
Dinophysis hastata Stein 1883: pl. 19, fig. 12.—Kofoid and Skogsberg 1928: 261, figs. 32, 33.—Böhm 1936: 17, fig. 6.—?Rampi 1940: 262, fig. 40.—?Gaarder 1954: 19, fig. 19.—Halim 1960: pl. 2, fig. 4.—?Wood 1954: 199, fig. 47.—Abé 1967b: 76, fig. 25.
Dinophysis uracantha (Stein) Silva 1956: 356, pl. 3, fig. 5.

General

This is a medium sized species. In lateral view the body is irregular and asymmetrically oviform, gently convexed to subtruncate anteriorly, rounded to moderately tapering posteriorly and deepest near the middle. The length to depth ratio is 1.10–1.21:1. The longitudinal axis is deflected 0–6° ventrally.

The epitheca is 0.53–0.56 as deep as the hypotheca, slightly convexed while tending to be truncated, highest at or slightly dorsal to the middle, and distinctly below the distal margin of the anterior cingular list. The cingulum is flat to slightly convexed; its width is 1.33–1.67 the epithecal height. It tends to be slightly narrower ventrally than dorsally. The posterior cingular list is ca. 0.09–0.12 the body length form the apex. The dorsal margin of the hypotheca is generally moderately and uniformly convexed though it may be somewhat flattened posteriorly. The ventral margin is moderately and uniformly convexed to somewhat flattened anteriorly and/or posteriorly. The posterior end is broadly rounded to somewhat tapered. In ventral view the body is narrowly obovate to broadly subelliptical, widest near the middle and typically more narrowly tapered posteriorly than anteriorly. In magacytic individuals the body broadens laterally, especially on the dorsal side and at the posterior end resulting in a subtrapezoidal shape in ventral view. The length to width ratio is 1.47–1.92:1 (1.38–1.56:1 in magacytic individuals), the depth of the cingulum to the transdiameter is 1.70–2.00:1 (1.40–1.52:1 in megacytic individuals).

The anterior cingular list is 2.66–3.26 the width of the cingulum; the posterior is 0.60–0.82 the width of the anterior. These lists are inclined anteriorly, the



FIGS. 46–59. *Dinophys hastata.* 46 and 47, an individual from sample BN-12; 48 and 49, two specimens from sample P-16B; 50 and 51, an individual from sample BN-15; 52 and 53, a megacytic individual from sample BN-9; 47, 51, and 53 are in ventral view, the others are in right lateral view. 54–59, thecal plates: 54, epithecal plates showing E_2, E_3, Po, and Ppl with omission of the anterior cingular list; 55, left portion of epitheca seen from the right and showing the parasagittal list of E_2; 56, cingular plates; 57, ventral region of H_3 with S_d, S_p, H_1, and H_4; 58, sulcal plates with E_1, E_4, and C_1 which has started to tear, from individual illustrated in Fig. 48; 59, C_3 as seen from within and exhibiting a rare spine, from an individual similar to the one illustrated in Fig. 48. 54–57 are from the individual illustrated in Figs. 46 and 47.

first 26–33°, the latter 22–32° and either may be inclined slightly more than the other. Simple, nearly complete radial ribs of weak to moderate strength are present in the anterior list while the posterior list is generally smooth. The latter may have irregular, poorly formed ribs in more mature individuals. The left sulcal list is 0.61–0.67 the body length and widest posteriorly. The ventral margin is irregularly oblique with concave and convex portions while the posterior is somewhat concave to rather sigmoid. The free margin forms an acute angle of

as much as 53° at R_3. R_2 is 0.18–0.25, R_3 0.52–0.57 the greatest body depth. The ribs of this list are moderately to well developed. R_1 and R_2 are generally straight to slightly concave anteriorly; R_3 is moderately concave posteriorly, straight in the proximal 2/3 and then concave posteriorly, or sigmoid with the posterior concavity distal. R_3 is inclined 30–38° posteriorly. The left sulcal list is most generally smooth but may have distinct ribbing in the posterior portion, with a tendency to become reticulate near the base. One megacytic specimen was observed with pronounced reticulation over most of the area between R_2 and R_3 but smooth behind R_3. The right sulcal list ends near R_2, is subuniform in width throughout the greater part of its length, rounded or gradually tapering posteriorly and smooth. Near the antapex there is an acute, subtriangular list, the posterior sail, which is inclined 28–37° ventrally. It is ca. 0.61–0.75 as wide at the base as it is long. The posterior sail possesses three or more proximal ribs which are fused to form a rather strong distal spine. The ribs are quite pronounced, typically both marginal and interposed; or the most distinct rib may be medial. Ventrally, this list is slightly to rather strongly concave or sigmoid. The dorsal margin is nearly straight or weakly concaved, convexed, or sinuous; as a whole the list is somewhat curved toward the ventral side. Its length is 0.35–0.49 the body depth. In one megacytic individual (Figs. 52 and 53) this list is more spine-like and has some areolation.

Thecal Plates

The epitheca is narrow and rather elongated dorsoventrally. Each dorsal plate is rather D-shaped in apical view. The sagittal suture is composed of indistinguishable to small, rounded or comparatively large, pointed denticles. The ventral notch in each plate is relatively large, especially in E_3 which in the dissected state might be confused with E_2. These plates are smooth, each has a row of pores near the perimeter and a few scattered pores medial to the row. A parasagittal list may be present on at least one of these dorsal epithecal plates, once such a list was seen on E_2. The ventral epithecal plates are quite similar, however E_1 has two pores, E_4 has one.

The pore plate (Po) is relatively large, thick on at least one margin, and is subelliptical, rhomboidal or rather irregular shaped. It may be notched on the thick margin as part of the sagittal suture which connects to that of E_3. There also may be a notch on the ventral side as part of the apical pore.

The pore platelet (Ppl) is rhomboidal or somewhat comma-shaped, and thick, and may be about as large as Po but typically it is smaller. A small spine was observed once, it is believed to run confluent with the anterior cingular list. (This may also be the case for similar structures in *D. doryphora.*) Ppl is in contact with Po on the right dorsal portion, E_1 ventrally and to the right and E_2 on the left and dorsal sides. Though generally not present, a pore was seen in one instance. The apical pore appears to be enclosed by E_1, Po, and possibly Ppl.

Compared to *D. doryphora*, the epitheca is small while Po and Ppl are large; thus, with the ventral epithecal plates, Po and Ppl occupy relatively large ventral notches in E_2 and E_3.

The cingular plates are smooth, C_1 is somewhat longer than C_4; it broadens ventrally and may end in a posteroventral denticle. C_4 sometimes has an anterior list which is probably confluent with that of the epitheca. The list varies in size and shape. All four plates have a row of pores near the anterior and posterior margins.

The dorsal hypothecal plates have small, rounded to relatively large, pointed denticles along with sagittal suture. These plates are smooth except for small to medium sized poroids. The poroids are most distinct near the middle of the plate and fade toward all margins where they are generally absent. The ventral hypothetical plates together are ca. 0.55–0.59 and length of the hypotheca. H_4 is 1.20–1.49 the length of H_1. Each plate has a row of pores.

The sulcus is somewhat shorter than H_1 and H_4 together; it extends to about half way down H_4. There are no lists on the sulcal plates. The anterior plate is subequal in length to C_1. It is narrow and elongated, the anterior margin is oblique, the posterior truncated, the left margin is concaved anteriorly and posteriorly, the right is sigmoid. The left sulcal plate has one pore. The right sulcal plate has two pores.

The posterior sulcal plate is somewhat longer than H_1, shorter than H_4, and 0.24–0.30 the body length. The left apophysis is about of equal length to the right, it may bear denticles which extend down the anterior 0.40–0.45 of the left margin. This narrow, elongate plate has subparallel sides and is gently convex to subtruncate posteriorly. There is an irregular row of pores down each margin.

The nucleus is difficult to distinguish, it is generally found in the posterodorsal quadrant of the body. Oil droplets may be found in the cell.

Dimensions

Body length, 66–69; total length, 84–90; epithecal depth, 30–33; hypothecal depth, 56–60; transdiameter, 23–24; body width, 36–45; maximum width of the left sulcal list, 25–31.5; R_1–R_2 15–17(23–28); R_2–R_3 17–21(38–45); R_3–PS 33–37(41–49).

Six specimens (plus four magacytic individuals) were measured and five (plus two) were examined for their plate morphology.

Variations

As a whole the specimens examined in this study are quite similar but there are what may be considered significant variations. The more general and obvious variations are in the body shape, and the structure of the left sulcal list and the posterior sail. One individual (Figs. 50 and 51) differed in the size of the poroids and in the relative width of the body. The latter character compares with that of Pavillard (1909, Fig. 4B). in all other (non-megacytic) specimens the ventral view is broadly subelliptical (Fig. 47). The literature is lacking in data related to this variation.

Though the plate characteristics (size and shape) from one individual to another agree reasonably well, there are some obvious differences. A list on the right ventral cingular plate and an anterodorsal spine (Fig. 59) on the dorsal

cingular plates were seen in different individuals. There also may be a parasagittal list on at least one dorsal epithecal plate. In one instance (plus in one megacytic specimen) there were five cingular plates, the right series having three rather than two.

The individuals examined here have a rather high anterior cingular list, the epitheca is never visible above the distal margin as Kofoid and Skogsberg (1928: 262) report. The posterior sail also is unlike those figured by Kofoid and Skogsberg. The figure presented by Abé (1967b: fig. 25) is quite similar to those presented here. A comparison with the work of Böhm (1936) leads to the suggestion that the individuals here are between his northern and southern forms, being somewhat closer to the latter.

Remarks

The specific allocation of these specimens is tentative as it is believed that future analyses of other variations within this species will provide further evidence for the presence of more than one entity. As mentioned in the introduction, previous workers believe *Dinophysis hastata* to be a collective species. Whether this is so, has not been shown absolutely but it is supported by several facts: no one has illustrated an individual which compares well with Stein's original figure; several variations of *D. hastata* are illustrated in the literature; the new species described herein could have been considered as *D. hastata*, without a careful analysis; and analyses of thecal plates within the "hastata" group reveal apparent specific differences. It is suggested therefore, that further studies will result in descriptions of additional new species.

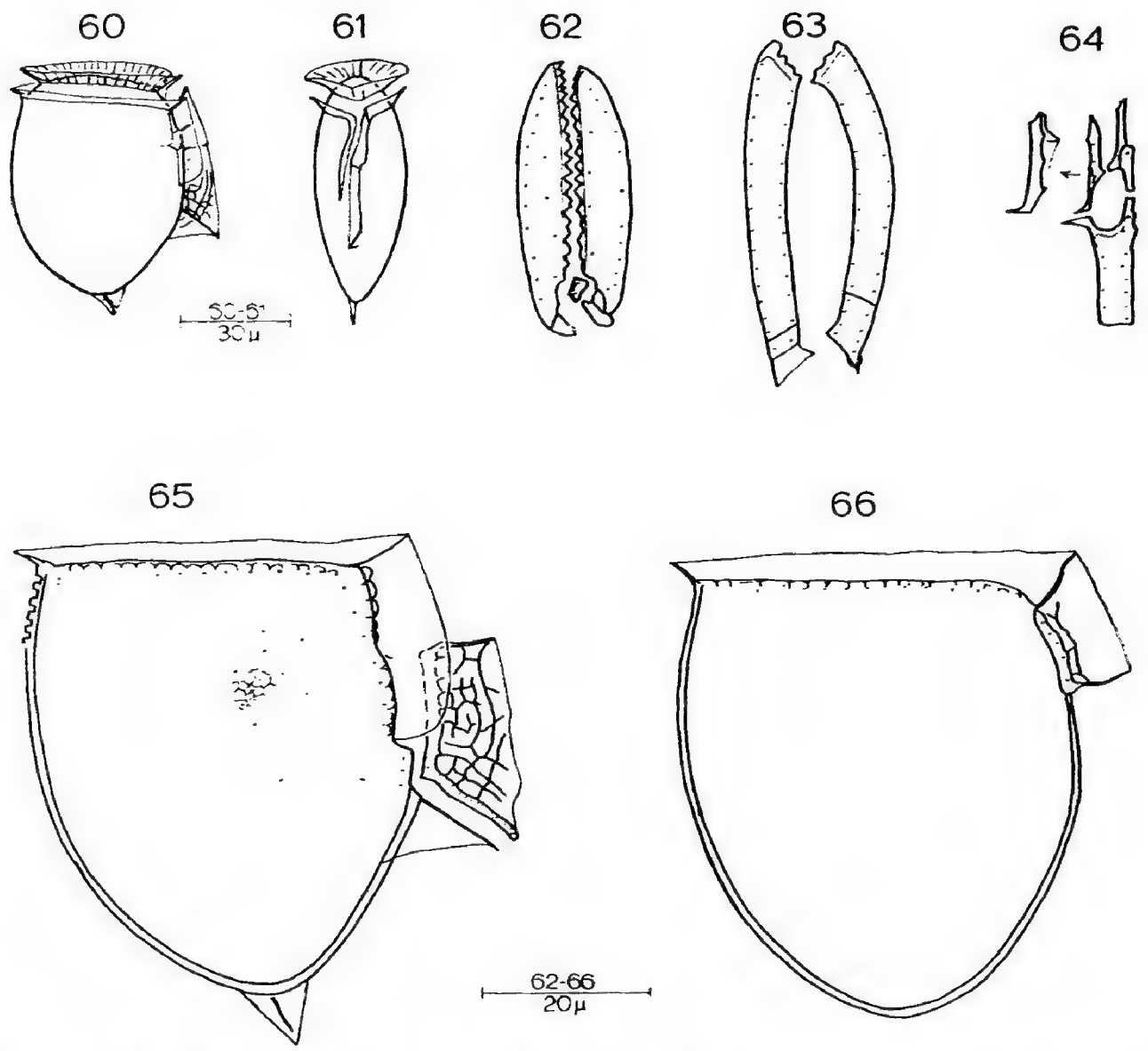
Dinophysis odiosa (Pavillard) Tai and Skogsberg
Figures 60–66

Phalacroma odiosum Pavillard 1931: 42, pl. 2, fig. 1—Rampi 1940: 258, fig. 29.
Dinophysis odiosa (Pavillard) Tai and Skogsberg 1934: 448, fig. 8.—Gaarder 1954: 20, fig. 20b.

General

The body of this medium sized species is subobovate in lateral view, somewhat truncate anteriorly, asymmetrically and narrowly rounded posteriorly, and deepest near the middle. The length to depth ratio is 1.30:1. The longitudinal axis is deflected 5° ventrally.

The epitheca is 0.65 as deep as the hypotheca, symmetrical, gently convexed, highest near the middle and slightly below the distal margin of the anterior cingular list. The cingulum is slightly concaved to slightly convexed; its width is three times the height of the epitheca. It is subuniform in width throughout its dorsoventral length. The posterior cingular list is 0.13 the body length from the apex. The hypotheca is somewhat asymmetrical. Its dorsal margin is rather flat anteriorly to moderately convexed posteriorly. The ventral margin is gently convexed anteriorly with a broad curve near R_3 and rather flat posteriorly. The pos-



FIGS. 60–66. *Dinophysis odiosa*. 60 and 61, right lateral and ventral view of the one specimen, from sample MP-1. 62–66, thecal plates from the individual represented in Figs. 60 and 61: 62, epitheca with omission of the anterior cingular list; 63, cingular plates; 64, sulcal plates; 65, H_3 and H_4; 66, H_2 as seen from within, and H_1.

terior end is asymmetrically tapered and considerably narrower than the anterior. In ventral view the body is narrowly subelliptical with rather symmetrical sides and widest near the middle. The posterior end is more narrowly rounded than the anterior. The length to width ratio is 2.40:1; the depth of the cingulum to the transdiameter is 1.90:1.

The anterior cingular list is 1.17 the width of the cingulum; the posterior is 0.57 the width of the anterior. Both lists are inclined anteriorly; the anterior 30° the posterior 18°. The latter is noticeably more inclined in ventral view. Fine, complete to incomplete, simple, radial ribs are present on the anterior list while the posterior is smooth. The left sulcal list is 0.58 the body length and widest posteriorly. Its ventral margin is gently convexed, the posterior margin is nearly straight to slightly concave. An angle of ca. 86° is formed at R_3. R_2 is 0.14, R_3 0.28 the greatest body depth. The ribs of this list are weak or of moderate strength. R_1 and R_2 are nearly straight to concave forward; R_3 is straight to slightly concave posteriorly and inclined posteriorly 33°. The left sulcal list has weak, irregular ribbing which forms a reticulation over much of its area. The right sulcal list

(seen with difficulty) ends somewhat in front of R_3; it is subuniform in width throughout most of its length, rounded posteriorly and smooth. The posterior sail is comparatively small, triangular, located ventral to the midline and inclined 5° ventrally. Its base is 1.33 its length. It has a general thickened appearance and a medial rib; the margins are rather straight. The length of this list to the body depth ratio is 0.13:1.

Thecal Plates

The thecal wall is of moderate thickness and strength. The epitheca is narrowly subelliptical in apical view. The dorsal epithecal plates have small to medium, rounded to pointed denticles along the sagittal suture. Both plates are smooth over most of their area; each has a row of pores near the outer margin and four pores near the inner margin. There is a very narrow parasagittal list on at least a portion of E_2. The ventral epithecal plates are somewhat elongated and appear to lack pores.

The pore plate (Po) is subrectangular to trapeziform. It appears to form the dorsal margin of the apical pore. There also seems to be a pore in the pore plate, a character not observed in the other species of this study.

The pore platelet (Ppl) is nearly as large as the pore plate, rather irregular-shaped, and may form the left ventral portion of the apical pore. Ppl touches E_1 ventrally, E_2 to the left and dorsally, and Po to the right. The left half of the epitheca was lost before separation of Ppl could be observed; its presence is not questioned however as the suture line, position, and shape closely resemble these features in other species. The apical pore appears to be enclosed by E_1, Po and Ppl.

The cingular plates are smooth. C_1 is more than three times longer than C_4; it broadens somewhat ventrally, especially posteroventrally where it ends in a small denticle. C_4 has a relatively broad list along its ventral margin. There is a row of pores near the anterior and the posterior borders of the cingular plates except in C_4 which has only one pore near each of the two margins.

The dorsal hypothecal plates have small to medium, truncate to pointed denticles along the sagittal suture. Most of their surface is covered with an irregular polygonal reticulation. Though it is distinct under oil immersion, under lower magnification this reticulation may appear as closely knit poroids. The ventral hypothecal plates together are 0.50 the length of the hypotheca. H_4 is 1.50 the length of H_1. H_1 has five pores in a row; the number in H_4 was not ascertained.

The sulcus is slightly shorter than H_1 and H_4 together, it extends 0.58 of the way down H_4. The anterior sulcal plate is concave anteriorly and posteriorly on the left margin where it abuts C_1 and S_s respectively. The right margin is concave to accommodate S_d. The left sulcal plate has one pore. The right sulcal plate (S_d) is 1.36 the length of S_a and 0.82 the length of S_p. It has an outward directed process at the base of the posterior extension supporting a small list which is oriented anteroposteriorly over most of the length of the plate. Two pores are present.

The posterior sulcal plate (S_p) is subequal to or slightly shorter than H_4, and 0.24 the body length. There is a short outward directed process, at the base of the

right apophysis, which appears to support a narrow list along the concave anterior margin of the plate. The left apophysis is somewhat longer than the right and has three small denticles. Behind the anterior apophyses the lateral margins are subparallel and the posterior is truncate. There are about seven pores near the left margin and fewer near the right.

The cytoplasmic structure was distorted such that the nucleus could not be delimited. Several oil droplets were present.

Dimensions

Body length, 60; total length, 66; epithecal depth, 30; hypothecal depth, 46; transdiameter, 19.5; body width, 25; maximum width of the left sulcal list, 12; R_1–R_2 11(17); R_2–R_3 15(24); R_3–PS 30(34).

The only available specimen was measured and examined for its plate morphology.

Except for the individual reported by Gaarder (1954) this specimen differs from those previously described in having a shorter posterior sail. The shape of the body and of the left sulcal list are rather different from those illustrated by Rampi (1940) and Gaarder (1954).

In regards to the thecal plates, the relative length of H_4 versus H_1 is less, while S_p versus the body length is greater than that found by Tai and Skogsberg (1934: 450). Other variations, the most obvious of which is the presence of a list along the ventral margin of C_4, seem to be within the limits of variation for a species. This report provides supplementary information, mainly measurements and ratios, to that given by Tai and Skogsberg.

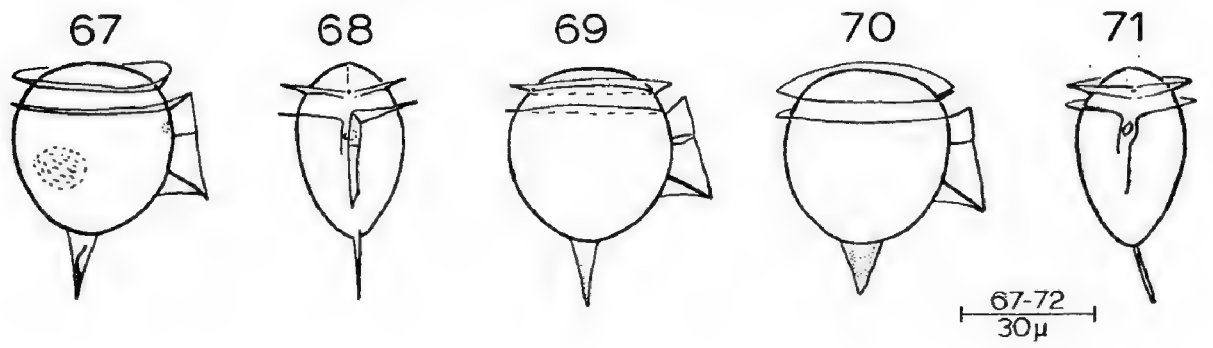
Dinophysis paulseni (Schiller) Balech
Figures 67–68

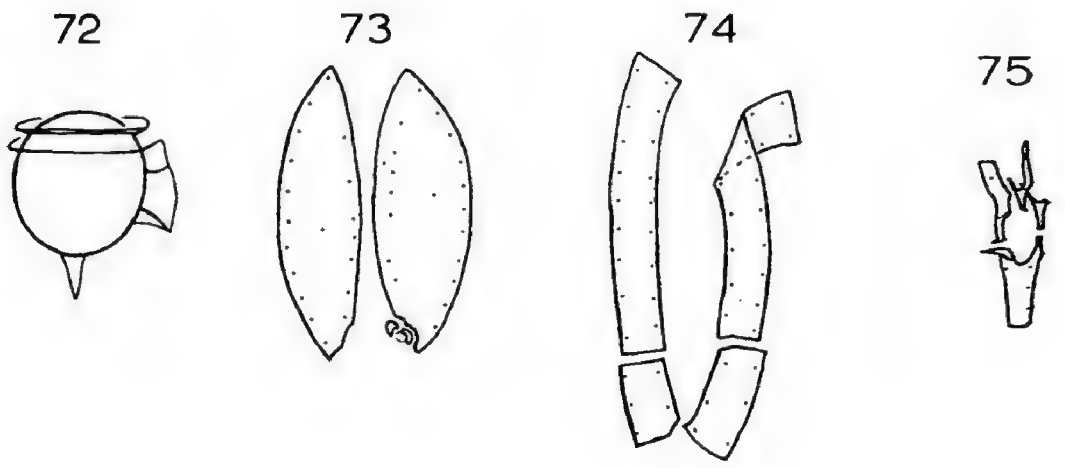
Phalacroma paulseni Schiller 1928: 67, fig. 29.
Phalacroma mucronatum Kofoid and Skogsberg 1928: 172, fig. 22: 4, 6, 8.—Hasle 1960: 31, fig. 23.—Wood 1963: 5, fig. 8.
Dinophysis paulseni (Schiller) Balech 1967c: 88, pl. 1, figs. 13–19.

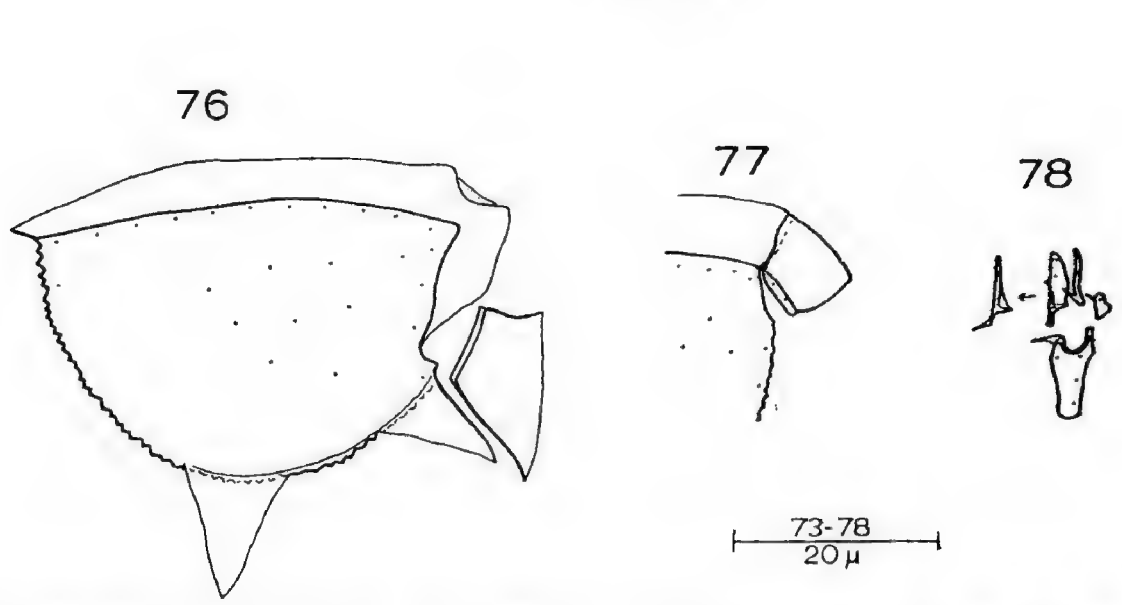
General

The body of this small species is broadly elliptical to subrotund in lateral view and deepest near the middle. The length to depth ratio is 1.00–1.08:1. The longitudinal axis coincides with the midline.

The epitheca is 0.76–0.87 as deep as the hypotheca, moderately and evenly convexed, highest near the middle and well above the anterior cingular list. The cingulum is slightly convexed; its width is 0.67–1.09 the height of the epitheca. It is subuniform in width throughout its dorsoventral length. The posterior cingular list is ca. 0.26–0.39 the body length from the apex. The hypotheca is rather symmetrical, the dorsal and ventral margins are moderately and evenly convexed. The posterior end is evenly rounded and tends to be slightly narrower than the anterior. In ventral view the body is somewhat narrowly subobovate with rather







FIGS. 67–78. *Dinophysis paulseni*. 67 and 68, an individual from sample BN-16; 69 and 71, an individual from sample BN-10; 70, another individual from BN-10; 72, an individual from sample BN-16; 68 and 71 are in ventral view, the others are in right lateral view. 73–78, thecal plates: 73, epithecal plates showing E_2, E_3, Po, and Ppl with omission of the anterior cingular list; 74, cingular plates, C_2 is folded; 75, sulcal plates; 76, H_3 and H_4; 77, anteroventral portion of H_2 from within and H_1; 78, sulcal plates. 73–75 are from the individual illustrated in Figs. 67 and 68; 76–78 are from the individual illustrated in Fig. 70.

symmetrical sides and is widest slightly anterior to the middle. The narrower posterior end broadens to make the ventral view broadly subelliptical in magacytic individuals. The length to width ratio is 1.50–1.62:1 (1.20–1.38:1 in megacytic individuals); the depth of the cingulum to the transdiameter is 1.48–1.67:1 (1.11–1.36:1 in megacytic individuals).

The anterior cingular list is 0.83–1.25 the width of the cingulum; the posterior is 0.60 the width of the anterior. These lists are typically inclined anteriorly, the

first 16–20°, the latter 0–23°. They tend to be more inclined ventrally than dorsally. Both cingular lists are smooth. The left sulcal list is 0.47–0.51 the body length and widest posteriorly. The distal margin of the anterior portion is straight to slightly convexed. Between R_2 and R_3 it is straight, slightly convexed, or sigmoid. The posterior margin is generally slightly concaved. An angle of 45–69° is formed at R_3 distally. R_2 is 0.14–0.17, R_3 0.31–0.33 the greatest depth of the body. The ribs of this list are rather weakly developed. R_1 is straight to slightly concave anteriorly; R_2 slightly concave to convex anteriorly; R_3 is straight to slightly concave posteriorly. R_2 is inclined 26–40.5° posteriorly. The left sulcal list is typically smooth and delicate but an irregular rib may occasionally be present. as seen near R_2 in Fig. 69. The right sulcal list is delicate and not readily discernable *in situ*. Upon dissection and with the use of trypan blue, it was found to end near the posterior end of the sulcus just in front of R_3; it is subuniform in width in the anterior 0.50–0.58 and then tapers rather sharply. This list is smooth. Near the antapex there is an acute, triangular list, the posterior sail. It is on or somewhat dorsal to the midline and inclined from 4.5° dorsally to 3° ventrally. Its base is 0.43–0.75 its length. This list is smooth and delicate, or has some thickening with a tendency to form a spine. One megacytic individual was observed with a straight medial spine, bifurcated at the base. The length of this list to the body depth is 0.32–0.42:1.

Thecal Plates

The thecal plates are thin and delicate or they are of moderate strength. The epitheca is subelliptical in apical view. The sagittal suture margin is rather smooth and gently undulating, or has small to medium sized, rounded to pointed denticles. In one slightly megacytic individual, the denticles were as described by Balech (1967c: 88, fig. 16): ". . . de denticulado triangular irregular, de base muy ancha y en general con bordes crenulados." The dorsal plates are smooth and each has a row of small pores near the perimeter plus up to three medial pores.

The pore plate (Po) is small and irregular to somewhat comma-shaped. The concaved portion marks part of the boundary of the apical pore. This plate is medial, being as much or more in the ventral notch of E_3 as in E_2. Besides the two dorsal plates, it touches both Ppl and E_1.

The pore platelet (Ppl) is slightly smaller than Po and it is irregularly C-shaped. It lies ventrally and to the left of Po in the ventral notch of E_2 and touches E_1 ventrally. In two individuals, margins of the pore platelet extended around (or nearly so) the apical pore and appeared to support a membrane completely covering the apical pore. If not as above, the apical pore is enclosed by Po. Ppl and E_1.

The cingular plates are smooth. The ventral plates are subrectangular and C_1 is slightly longer than C_4. C_1 has a slight ventral broadening. The anteroventral margin of C_4 is oblique to accommodate E_4. All four plates have a row of pores near the anterior and the posterior margins.

The dorsal hypothecal plates in particular may fold or tear under the mechanical stress of dissection. The margin along the sagittal suture is rather smooth and

without distinct denticles or it has small to medium-sized, rounded to pointed denticles. One slightly megacytic individual possessed denticles similar to those in its epitheca described above. Closely knit, minute poroids on the dorsal plates are best seen under oil immersion. The ventral hypothecal plates are ca. 0.47–0.51 the length of the hypotheca. H_4 is 1.27–1.54 the length of H_1. H_1 has two pores, H_4 has three in a row.

The sulcus is ca. 1.12–1.24 the length of the ventral hypothecal plates together. It extends to near the posterior end of H_4. The left plate (S_s) is irregular-shaped and may have one pore. The right sulcal plate (S_d) in at least some individuals has an outward directed rib at the base of the posterior extension. This rib, with the right margin of the plate supports a small triangular list which may be seen with an application of trypan blue. One pore is present.

The posterior sulcal plate (S_p) is subequal to or slightly longer than H_4 and 0.23–0.26 the body length. The ventral face is somewhat concave anteriorly. The left apophysis is the longer, its left margin tends to be concave and without denticles. Posterior to the anterior apophyses, the left margin is concave or convex, the right is concave. The posterior is truncate or slightly convex. There are two to three pores near the left and one near the right margin.

The nucleus is oviform and in the dorsomedian portion of the body.

Dimensions

Body length, 39; total length, 51–55; epithecal depth, 28.5–32; hypothecal depth, 36–39; transdiameter, 21–24; body width, 24–26; maximum width of the left sulcal list, 12; R_1–R_2 4–6(8–9); R_2–R_3 9(13–15); R_3–PS 22–27(32–37).

Three specimens (plus six megacytic individuals) were measured and three (plus one) examined for their plate morphology.

Variations

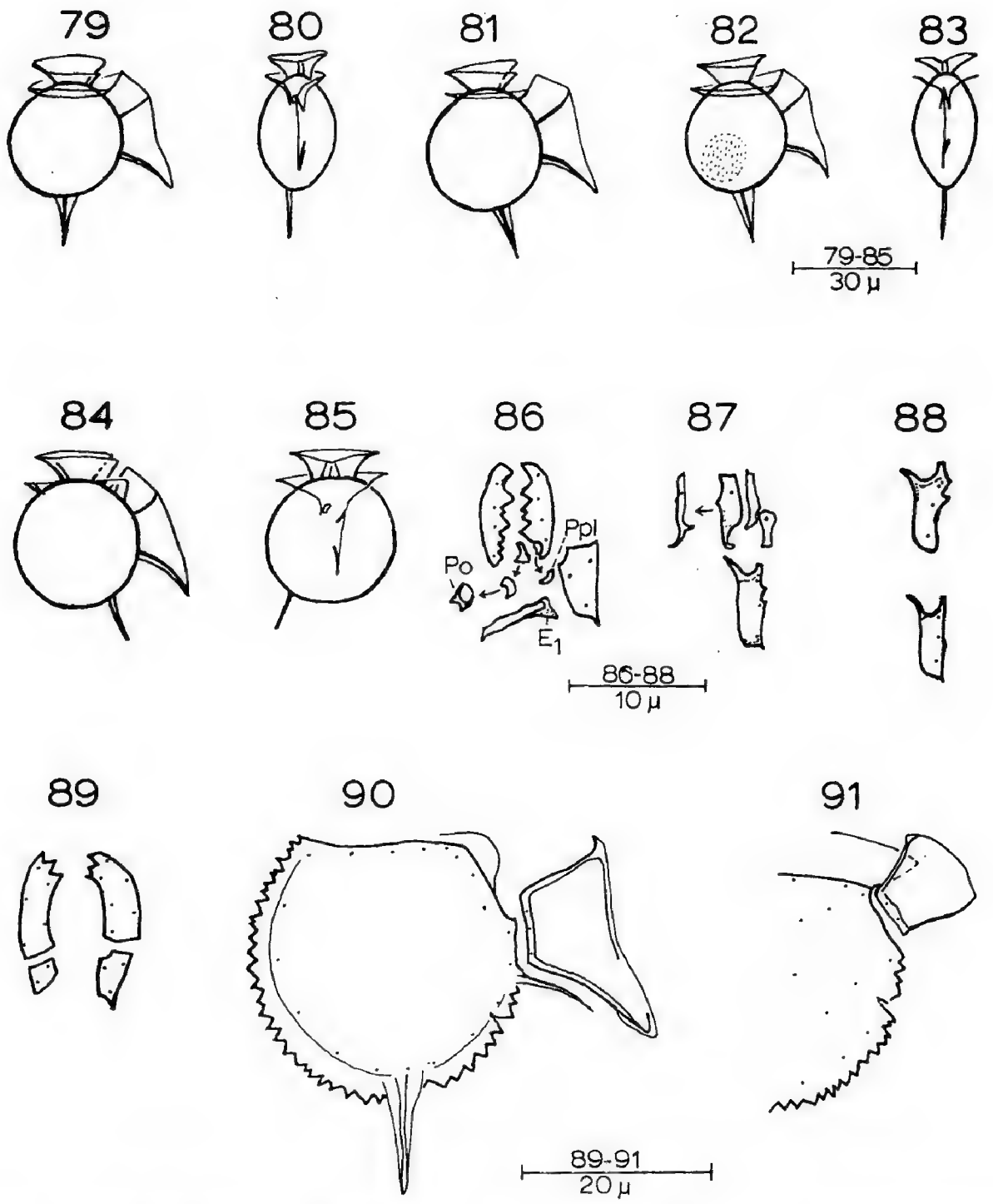
The specimens in this study are quite similar to those of previous studies, especially Balech's (1967c). The individual illustrated by Wood (1963) appears to be comparatively rotund, has a smaller epitheca, and lacks the small portion of the left sulcal list behind R_3. Hasle (1960) illustrated an individual which appears to be somewhat rotund and has a short R_3. These individuals were probably megacytic.

In regards to the thecal plates, this report is in good agreement with that of Balech (1967c); however, the present paper provides supplementary information to that given by him, mostly in the details of the thecal description.

Dinophysis paulseni differs from its closest relative, *D. doryphora*, in its smaller size and in the subcircular shape of its body in lateral view (see Kofoid and Skogsberg 1928: 174). Their close relationship is borne out by a comparison of thecal plates which are very similar in proportion and shape.

Dinophysis pusilla Jörgensen
Figs. 79–91

Dinophysis pusilla Jörgensen 1923: 33, fig. 44.—Balech 1967c: 89, pl. 1, figs. 20–24.



FIGS. 79–91. *Dinophysis pusilla.* 79 and 80, an individual from sample BN-16; 81, an individual from sample P-14F; 82 and 83, an individual from sample P-14G; 84 and 85, a megacytic individual from sample BN-22; 80, 83, and 85 are in ventral view, the others are in right lateral view. 86–91, thecal plates: 86, epithecal plates with omission of E_4 and the lists of E_2 and E_3, C_1 is shown to compare the relative size; 87, sulcal plates; 88, top S_p is from individual illustrated in Fig. 81, lower S_p is from individual illustrated in Figs. 82 and 83; 89, cingular plates; 90, H_3 with a small tear and H_4; 91, ventral portion of H_2 with a small tear and H_1. 86, 87, and 89–91 are from the individual represented in Figs. 79 and 80.

General

The body of this small species is subrotund to slightly elliptical in lateral view and deepest near the middle. The length to depth ratio is 1.02–1.13:1. The longitudinal axis is on the midline or deflected 3° to either side.

The epitheca is 0.24–0.29 as deep as the hypotheca, moderately convexed, highest near the middle, and well below the distal margin of the anterior cingular list. The cingulum is slightly convex its width is 3–4 times the height of the

epitheca. It is subuniform in width throughout its dorsoventral length. The posterior cingular list is 0.11–0.15 the body length from the apex. The hypotheca is quite symmetrical, moderately convexed throughout; the dorsal margin may be slightly more convexed than the ventral. The posterior end tends to be deeper than the anterior. In ventral view the body is lenticular to subelliptical with rather symmetrical sides and widest near the middle. The posterior end may be slightly narrower than the anterior. The body broadens in megacytic individuals to become subelliptical to rather rotund in ventral view. Thus the body as a whole may become nearly spherical. The length to width ratio is 1.38–1.69:1 (1.00–1.36:1 in magacytic individuals); the depth of the cingulum to the transdiameter is 1.25–1.74: (1.16–1.41:1 in megacytic individuals).

The anterior cingular list is 2.00–2.67 the width of the cingulum; the posterior is 0.38 the width of the anterior. The anterior inclination of the first is 32–40°, of the latter it is 13–28°. The anterior list is somewhat funnel-shaped. Both cingular lists are smooth. The left sulcal list is 0.50–0.60 the body length and widest near R_3. The distal margin of the anterior portion is oblique and straight; between R_2 and R_3 it is somewhat sigmoid; the very narrow posterior portion is slightly concaved. The free margin forms an angle of ca. 30–37° at R_3. R_2 is 0.32–0.39, R_3 0.54–0.64 the greatest body depth. The ribs of this list are moderately to well developed. R_1 is straight to slightly concaved anteriorly, R_2 is somewhat concaved anteriorly, R_3 is concaved posteriorly. R_3 is inclined 32–38° posteriorly. The left sulcal list is typically smooth; however, a marginal or submarginal rib between R_2 and R_3 may be observed under oil immersion. The right sulcal list is very small and is seen *in situ* only with difficulty; upon a dissection it was found to end near R_2, toward the posterior end of the sulcus. The distal margin is somewhat convexed to the oblique margin of H_3. *In situ*, this margin appears to be rather straight and to be about parallel to the longitudinal axis. This list is smooth The posterior sail is an acute, triangular list on or somewhat ventral to the midline and inclined 0–20° ventrally. Its base is ca. 0.34–0.46 its length. It is supported by a medial, comparatively well developed rib which may be bifurcated near the base. The fine margins of this list may be slightly thickened. The length of the posterior sail to the body depth is 0.43–0.50:1.

Thecal Plates

The thecal plates tend to be thin and delicate. The small epitheca is narrowly subelliptical in apical view. The dorsal epithecal plates have no distinct denticles or have medium to relatively large and pointed ones along the sagittal suture. These plates are smooth and each has three to four submarginal pores arranged in a row.

The pore plate (Po) is subtrapezoidal to somewhat comma-shaped. It bounds the right dorsal portion of the apical pore. There may be a small subrectangular list present.

The pore platelet (Ppl) is slightly smaller than the pore plate and is somewhat crescent-shaped. It forms the left dorsal portion of the apical pore. A small spine which appears to be confluent with the anterior cingular list may be present.

This plate communicates with E_2 to the left and dorsally, Po to the right and E_1 ventrally. Ppl tends to separate together with either Po or E_1 during dissection, its presence is therefore difficult to verify in a given individual.

The cingular plates are smooth. C_1 is 1.37–2.12 the length of C_4, it tends to broaden ventrally and then narrows to make the ventral margin rather oblique and end in a point posteroventrally. The short C_4 tends to have an oblique anteroventral margin where it touches E_4. The dorsal plates have two to three pores near the anterior border and three to four near the posterior. The ventral plates have one each near the anterior; C_1 has two and C_4 one near the posterior border.

The dorsal hypothecal plates may be without distinct denticles along the sagittal suture or they have medium to relatively large sized, pointed denticles. Closely knit, minute poroids can be seen under oil immersion. The small pores are larger than the poroids. The ventral hypothecal plates together are 0.49–0.59 the length of the hypotheca. H_4 is 1.33–1.45 the length of H_1. The latter has two pores, the former three or four in a row.

The sulcus is subequal in length to H_1 and H_4 together; it extends 0.33–0.50 the way down H_4. The anterior sulcal plate is concaved anteriorly and posteriorly on the left margin where it touches C_1 and S_s respectively. The left sulcal plate has one pore.

The right sulcal plate is subequal in length to both C_1 and H_1. The left margin tends to be slightly sigmoid, the right is concaved anteriorly and posteriorly where it abuts C_4 and H_3 respectively. An outward directed process at the base of the posterior extension may be present. Though not seen, there may be a minute list associated with this process. There is one pore present in S_d.

The posterior sulcal plate is slightly shorter than H_4 and 0.22–0.24 the body length. The left margin of this plate is without distinct denticles and nearly straight, or it may have two denticles which tend to be behind the left apophysis, and then it is concaved. There may also be an acute point at the left posterior corner. Posterior to the apophysis, the right margin is straight and then convexed at the right posterior corner. The posterior margin tends to be oblique. There are three pores near the left margin.

The nucleus is oviform and in the posterodorsal quadrant of the cell.

Dimensions

Body length, 27–29; total length, 39–42; epithecal depth, 6–8; hypothecal depth, 24–28; transdiameter, 9–12; body width, 16–21; maximum width of left sulcal list, 12–16; R_1–R_2 5–6(6–9); R_2–R_3 8(23–25); R_3–PS 16–17 (24–28.5).

Four specimens (plus four magacytic individuals) were measured and four examined for their plate morphology.

Variations

The specimens examined are rather similar, showing little variability on the whole. The most obvious variations are the position and inclination of the posterior sail. Dissection reveals obvious variability in the denticles along the sagittal suture and a lesser degree in the shape of C_1. Comparison of the sulcus, as

interpreted here, indicates some differences from that of Balech ,1967c, fig. 22). His figure appears to have two pores in both S_a and S_d while S_p has none. In this study these plates were found to have none, one, and three pores respectively. In addition to the apparent differences in pores, there is some difference in the shape of S_p, it appearing to be relatively longer in this study. More significant is that Balech found that S_a apparently does not communicate with the flagellar pore. The interpretation made in this study is that it does border the flagellar pore, the typical arrangement in *Dinophysis* (cf. Tai and Skogsberg 1934: 397).

Dinophysis schuetti Murray and Whitting
Figures 92–112

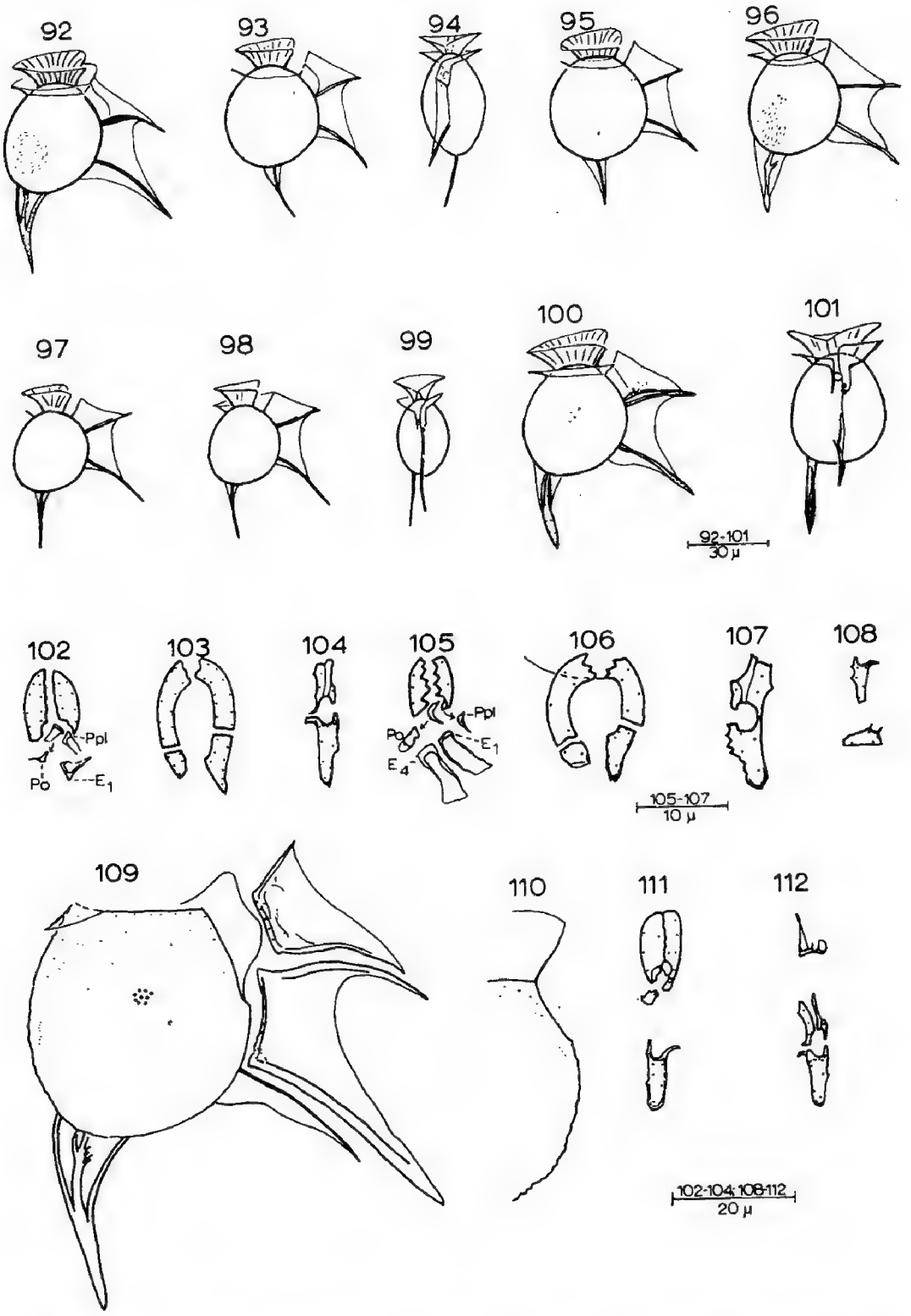
Dinophysis schuetti Murray and Whitting 1899: 331, pl. 31, fig. 10.—Wood 1963: 7, fig. 17.
Dinophysis schuttii (Murray and Whitting) Dangeard 1927: 382, fig. 44a.
Dinophysis schütti (Murray and Whitting) Kofoid and Skogsberg 1928: 296, fig. 40.—Rampi 1940: 263, fig. 39.—Halim 1967: 728, pl. 9, fig. 135.

General

The rather small individuals representing this species are nearly round to subelliptical in lateral view and deepest near the middle. The length to depth ratio is 1.04–1.17:1. The longitudinal axis is deflected 0–9° dorsally.

The epitheca is 0.18–0.38 as deep as the hypotheca, gently and evenly convex, highest near the middle and deep within the anterior cingular list. The cingulum is slightly convex; its width is 1.50–4.50 the height of the epitheca. It tends to be more or less the same width ventrally as dorsally. The posterior cingular list is 0.08–0.12 the body length from the apex. The hypotheca is symmetrical to somewhat asymmetrical. When not evenly rounded, it tends to be more convexed posterodorsally and on the ventral side. The posterior end tends to be deeper than the anterior. In ventral view the body is narrowly subelliptical to ovate with rather symmetrical sides and widest near the middle. The anterior end is more narrowly rounded than the posterior. Magacytic individuals are more broadly subelliptical to ovate in ventral view. The length to width ratio is 1.28–1.75:1 (1.14–1.37:1 in megacytic individuals); the depth of the cingulum to the transdiameter is 1.24–1.75: (1.14–1.48:1 in magacytic individuals).

The anterior cingular list is 2.50–4.50 the width of the cingulum; the posterior is 0.40–0.75 the width of the anterior. Both lists are inclined anteriorly, the first 32–42°, the later 14–36°. The anterior is always the more inclined and funnel-shaped. Nearly complete simple radial ribs of weak to moderate strength are present on the anterior list, the posterior is smooth. The left sulcal list is 0.61–0.79 the body length and widest generally at R_2. The oblique anterior portion is straight, gently concave, or sigmoid on the distal margin. Between R_2 and R_3 this margin is strongly concaved or sigmoid. The posterior margin is slightly concaved to sigmoid. An acute angle of ca.30–58° is formed at R_3. R_2 is 0.47–0.72, R_3 0.67–1.03 the greatest body depth. The ribs of the list are moderately to well developed, R_2 and R_3 often extend beyond the margin. R_1 is straight or slightly



FIGS. 92–112. *Dinophysis schuetti*. 92, an individual from sample BN-16; 93 and 94, an individual from sample P-14J; 95, an individual from sample BN-13; 96, an individual from sample BN-15; 97, an individual from sample P-14C; 98 and 99, an individual from sample P-14A; 100 and 101, a megacytic individual from sample BN-15; 94, 99, and 101 are in ventral view, the others are in right lateral view. 102–112, thecal plates; 102, epithecal region with omission of E_4 and the lists of E_2 and E_3; 103, cingular plates; 104, sulcal plates; 105, epithecal plates with omission of the lists of E_2 and E_3; 106, cingular plates showing a spine on C_2; 107, sulcal plates from within; 108, S_p from within and C_1 of individual represented in Fig. 98; 109, H_1, H_3, and H_4; 110, ventral portion of H_2 from within; 111, epitheca, with omission of the anterior cingular list, and S_p, all from within, from individual represented in Fig. 95; 112, E_1, Ppl, and the sulcal plates of the individual represented in Fig. 93. 102–104, 109, and 110 are from the individual represented in Fig. 92; 105–107 are from the individual represented in Fig. 97.

concaved anteriorly, rarely sigmoid. R_2 and R_3 are typically concaved posteriorly but may be nearly straight or sigmoid. R_3 is inclined posteriorly 10.5–43°. The left sulcal list appears to be smooth under low magnification but some structural differentiation may be seen under oil immersion. The right sulcal list appears to end near R_2. Upon dissection it may be seen to continue in a narrowed condition to near the end of the sulcus. It is subuniform in width and throughout the greater part of its length, rounded posteriorly, and smooth. The posterior sail is an acute subtriangular list, its base is near or several degrees dorsal to the midline. It is generally inclined ventrally (3–21°) but was 3° and 4° dorsally in two respective individuals. Its base is ca. 0.23–0.62 its length. There is always a rather strong medial rib which may extend beyond the distal end of the list. The margins may be delicate but tend to be thickened into ribs which fuse with the medial rib. Typically on the whole, the list is gently to moderately concaved ventrally; however, the medial rib may be rather straight. Its length is 0.50–0.83 the body depth.

Thecal Plates

The epitheca is subelliptical to subrectangular in apical view. Due to the small size of the plates and the relatively large anterior cingular list this portion of the theca is difficult to analyze. The dorsal epithecal plates are elongated, the left one generally has a distinctly larger ventral notch than the right. Larger individuals tend to have rather small, rounded to indistinct denticles along the sagittal suture while comparatively large and pointed denticles are present in the smaller individuals. These plates are smooth. Each one has two rows of minute pores in the larger specimens, only one row is present in the small individuals. The ventral epithecal plates apparently possess one pore each, though E_1 may have two.

The pore plate is subrectangular or subtrapezoidal. Though partially in the ventral notch of E_2, it may for the most part be in the ventral notch of E_3. This plate has a small, subrectangular list which is apparently always present. There is no pore in Po.

The pore platelet is about the same size as Po and more irregularly shaped. It lies to the left and sometimes ventral to Po in the ventral notch of E_2 and abuts E_1 ventrally. It too bears a list, similar to that of Po. In a given position, either of these plates may look like a small ventral epithecal plate. The apical pore is apparently enclosed by Po and Ppl, possibly also by E_1.

The cingular plates are smooth. C_1 is longer than C_4 and tends to broaden ventrally and then to taper to end in a denticle posteroventrally. When it is rather short, as in smaller individuals, this ventral portion makes up the greater part of the plate. There may be a minute list or spines on the anterior and/or dorsoanterior margins of the cingular plates. Pores are generally in two rows but are reduced in number in smaller individuals, C_4 in one having only one pore.

The hypotheca is noticeably delicate, the dorsal plates in particular tearing under the mechanical stress of dissection. The denticles along the sagittal suture are small and rounded to large and pointed. Smaller individuals tend to have

relatively large, pointed denticles. These plates are thin walled and smooth appearing though there are small, closely knit poroids present. The poroids are most distinct medially and fade to become absent toward the borders. The ventral hypothecal plates together are ca. 0.58–0.72 the length of the hypotheca. H_4 is 1.29–1.58 the length of H_1 which is subequal to or longer than C_1. A row of pores is present in each of these plates.

The sulcus is ca. 0.75 the length of the ventral hypothecal plates together. It extends to ca. 0.25–0.40 the way down H_4. There are no lists on the sulcal plates. The anterior sulcal plate is elongated, part of the anterior margin is oblique, the posterior appears to be truncated. The left margin is concaved anteriorly and posteriorly where it abuts C_1 and S_s respectively. The left sulcal plate has one pore, the right has two.

The posterior sulcal plate is subequal to or a little longer than H_1, shorter than H_4, and 0.25–0.30 the body length. The left apophysis is about equal to or slightly longer than the right. This plate is typically broader in the anterior portion (about half) where the left margin abuts H_1. This portion of the left margin has comparatively large denticles in small individuals and may be smooth in large ones. The right margin is nearly straight while the posterior is slightly oblique to convexed. Pores are present near the margins.

The nucleus is small, oviform, and in the posterodorsal quadrant of the body.

Dimensions

Body length, 28–42; total length, 48–71; epithecal depth, 5–13; hypothecal depth, 27–36; transdiameter, 9–14; body width, 20–25; maximum width of the left sulcal list, 15–28; R_1–R_2 7–12(18–36); R_2–R_3 10–16(23–36); R_3–PS (20–29(33–56).

Twelve specimens (plus four megacytic individuals) were measured and eight examined for their plate morphology.

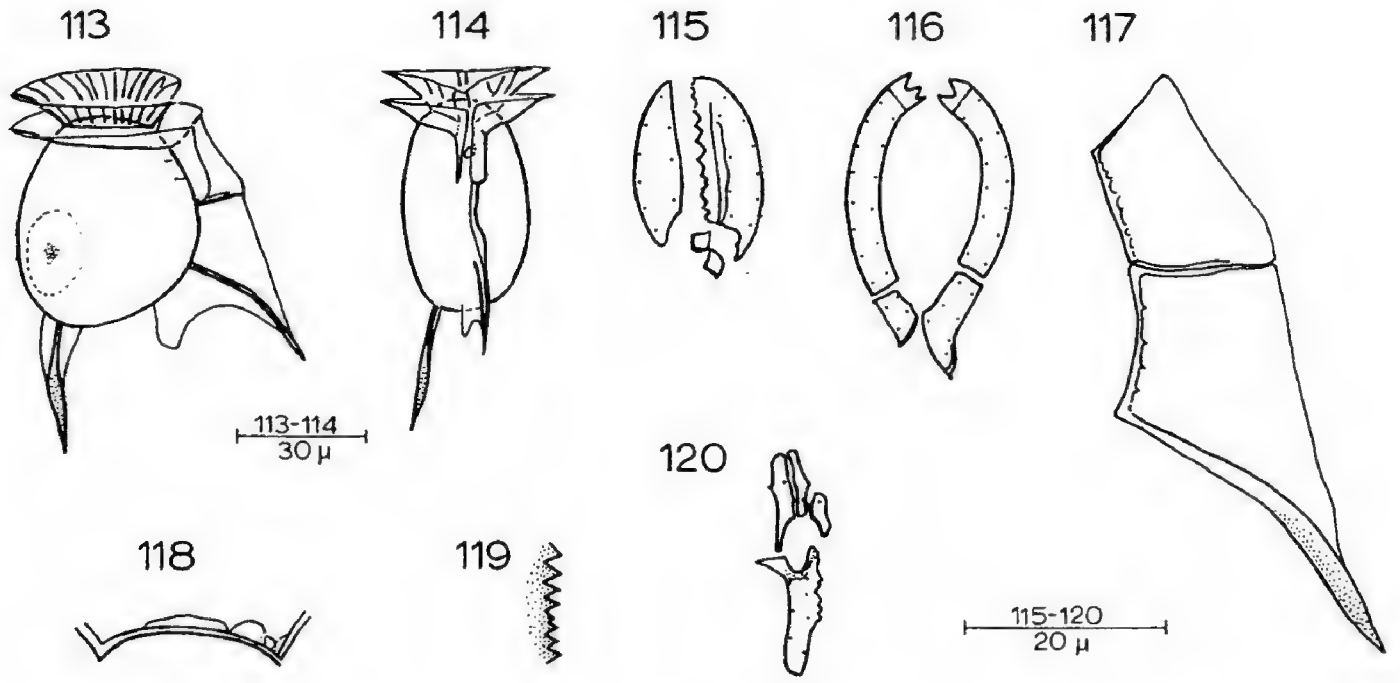
Variations

The variations of the specimens examined here are similar to those given by Kofoid and Skogsberg (1928: 299). Though there is some size class indicated here, it seems to be rather superficial. Upon gross examination (without dissection) the specimens could be placed into two groups : the smaller form is 28–33 μ long and 27–30 μ deep; the larger is 37–42 μ long and 33–36 μ deep. The most distinct differences (cf. Figs. 92 and 97) are the comparatively high anterior cingular list and the small epitheca of the smaller form. Intergradations of these characters are found, thus they cannot be considered of systematic value. These findings confirm the negative results discussed by Kofoid and Skogsberg (p. 300–01) in their attempt to establish a morphological difference between their two size classes.

Allowing for reasonable individual variations there does not seem to be justification for "splitting" this species on the basis of plate morphology. The more obvious differences *viz*, the size of the denticles along the sagittal suture and the number and distribution of pores in the dorsal epithecal plates, are attributed to size, not to species differences.

Dinophysis swezyi Kofoid and Skogsberg
Figures 113–120

Dinophysis swezyi Kofoid and Skogsberg 1928: 289, pl. 5, fig. 9; text fig. 39.



FIGS. 113–120. *Dinophysis swezyi*. 113 and 114, right lateral and ventral views of the one available specimen, from sample BN-15. 115–120, thecal plates from individual represented in Figs. 113 and 114: 115, epitheca showing E_2, E_3, Po, and Ppl with omission of the anterior cingular list; 116, cingular plates; 117, H_1 and H_4; 118, left portion of epitheca seen from the right and showing the parasagittal lists; 119, portion of dentiecls of H_3; 120, sulcal plates.

It should be noted that the larger form here is small compared to the larger size classes of Jörgensen (1923: 34) and Kofoid and Skogsberg (1928: 300). Dissection and analysis of the plate morphology of representatives of these large sized individuals would hopefully resolve the question.

General

The body of the medium sized individual representing this species is subovate in lateral view, asymmetrically rounded anteriorly, more broadly so posteriorly, and deepest near the middle. The length to depth ratio is 1.12:1. The longitudinal axis is deflected 9° dorsally.

The epitheca is 0.45 as deep as the hypotheca, gently to moderately convexed, highest dorsal to the middle and well below the distal margin of the anterior cingular list. The cingulum is flat to slightly convexed; its width is 1.33 the height of the epitheca. It is subuniform in width throughout its dorsoventral growth. The posterior cingular list is 0.11 the body length from the apex. The hypotheca is asymmetrical. The dorsal margin is gently convexed anteriorly and moderately so posteriorly. The ventral margin is moderately convexed with a tendency toward flatness anteriorly and posteriorly. The posterior end is asymmetrically rounded with the greatest convexity dorsal to the midline. In ventral view the body is narrowly subelliptical with rather symmetrical sides and widest near the middle. The posterior end is slightly more broadly rounded than the

anterior, probably due to the slightly magacytic condition of the cell. The length to width ratio is 1.57:1; the depth of the cingulum to the transdiameter is 1.28:1.

The anterior cingular list is four times the width of the cingulum; the posterior is 0.75 the width of the anterior. Both lists are inclined anteriorly, the anterior by 27°, the posterior by 13°. Simple, nearly complete and complete radial ribs of moderate strength are present on the anterior list, the posterior is smooth. The left sulcal list is 0.81 the body length and 2.33 wider posteriorly than anteriorly. Its ventral margin is oblique and with slightly sigmoid portions. The posterior margin is strongly sigmoid due to a rather tenuous lobe which is oriented nearly parallel to the midline. An angle of ca. 38° is formed at R_3. R_2 is 0.29, R_3 0.86 the greatest body depth. The ribs of this list are weak to strongly developed. R_1 and R_2 are nearly straight; R_3 is straight proximally and then moderately curved posteriorly and it is inclined posteriorly 36°. The left sulcal list is smooth; there are however, suggestions of rib formation at the base of the list. The right sulcal list appears to end near R_2; however, a very narrow continuation to near the posterior end of the sulcus may be seen during dissection. The list is subuniform in width throughout the greater part of its length, slightly sigmoid, rounded posteriorly, and smooth. The posterior sail is dorsal to the midline and inclined 6° ventrally. The width of its base is ca.0.31 its length. A well developed medial rib is present which extends well beyond the marginal lists. Though the rib and margins are slightly sigmoid, the posterior sail has a general ventral concavity. The length of this list is 0.72 the body depth.

Thecal Plates

The thecal wall is of moderate thickness and strength. The epitheca is subelliptical in apical view. The dorsal epithecal plates lack either distinct denticles or they have irregular, moderate to large, pointed ones along the sagittal suture. These plates are smooth, each has a row of pores near the lateral margin, and three or four pores near the sagittal line. There is a narrow parasagittal list on E_2 which appears to be lacking from the dorsal ¼. This tenuous list marks the edge of a narrow "growth" zone, evidence of the slight megacytic condition of the cell. The small ventral epithecal plates are compartively thick, the presence of pores was not confirmed.

The pore plate is relatively thick and subrectangular to elliptical. There is a list present, which though it is not a direct continuation of the parasagittal list of E_2, it is a counterpart. This list is ca. 1.3 μ above the cell wall at its highest point on the epitheca, unless it continues up the anterior cingular list.

The pore platelet is smaller than the pore plate, relatively thick, and also possesses a list. The list is about half as high as that on Po and appears to "overlap" it somewhat. Though not confirmed, Ppl appears to communicate with E_1 ventrally and possibly some to the right, E_2 to the left, and Po to the right and dorsally. An apical pore is believed to be present and enclosed by E_1, Po and Ppl.

The cingular plates are smooth save for the differentiating line marking the edge of a narrow "growth" zone on the dorsal plates. C_1 is 1.79 the length of C_4 and it broadens ventrally, especially posteroventrally, its ventral margin is ob-

lique. C_4 is subrectangular and may have a list ventrally. C_1 has three pores anteriorly and four posteriorly, C_4 has two and two respectively.

The dorsal hypothecal plates have medium to large, pointed denticles along the sagittal suture. Closely knit, small, tenuous poroids are present on both plates. The ventral hypothecal plates together are 0.66 the length of the hypotheca. H_4 is 1.33 the length of H_1. H_1 has three pores, H_4 has four or five in a row.

The sulcus is ca.0.84 the length of H_1 and H_4 together. It extends 0.37 of the way down H_4. The anterior sulcal plate is concaved anteriorly and posteriorly on the left margin where it abuts C_1 and S_s respectively. The left plate has one pore. The right sulcal plate is comparatively long, equal in length to C_1 and 0.80 the length of S_p. The anterior margin is oblique, the left is irregularly sigmoid, the right concaved anteriorly and posteriorly where it abuts C_4 and H_3 respectively. There is one pore present.

The posterior sulcal plate is elongated, 0.83 the length of H_4 and 0.28 the length of the body. The anterior 0.55 is broader where the denticulated left margin meshes with H_1. The posterior portion of the left margin and the right margin are slightly sigmoid but otherwise are nearly parallel. The posterior margin is oblique. There are four pores near the left and two near the right margin.

The nucleus is irregularly ellipsoidal and mostly in the posterodorsal quadrant of the cell. A distinctly polygonal network was observed throughout the nucleus. One oil droplet was seen posterior to the nucleus.

Dimensions

Body length, 47; total length, 79; epithecal depth, 19; hypothecal depth, 42; transdiameter, 21; body width, 30; maximum width of the left sulcal list, 28; R_1–R_2 12(21); R_2–R_3 15(42); R_3–PS 33(60).

The one available specimen, slightly megacytic, was measured and examined for its plate morphology.

This specimen compares well with those described by Kofoid and Skogsberg (1928). This study illustrates *D. swezyi* in ventral view and gives an analysis of the thecal plates for the first time.

Dinophysis uracantha Stein

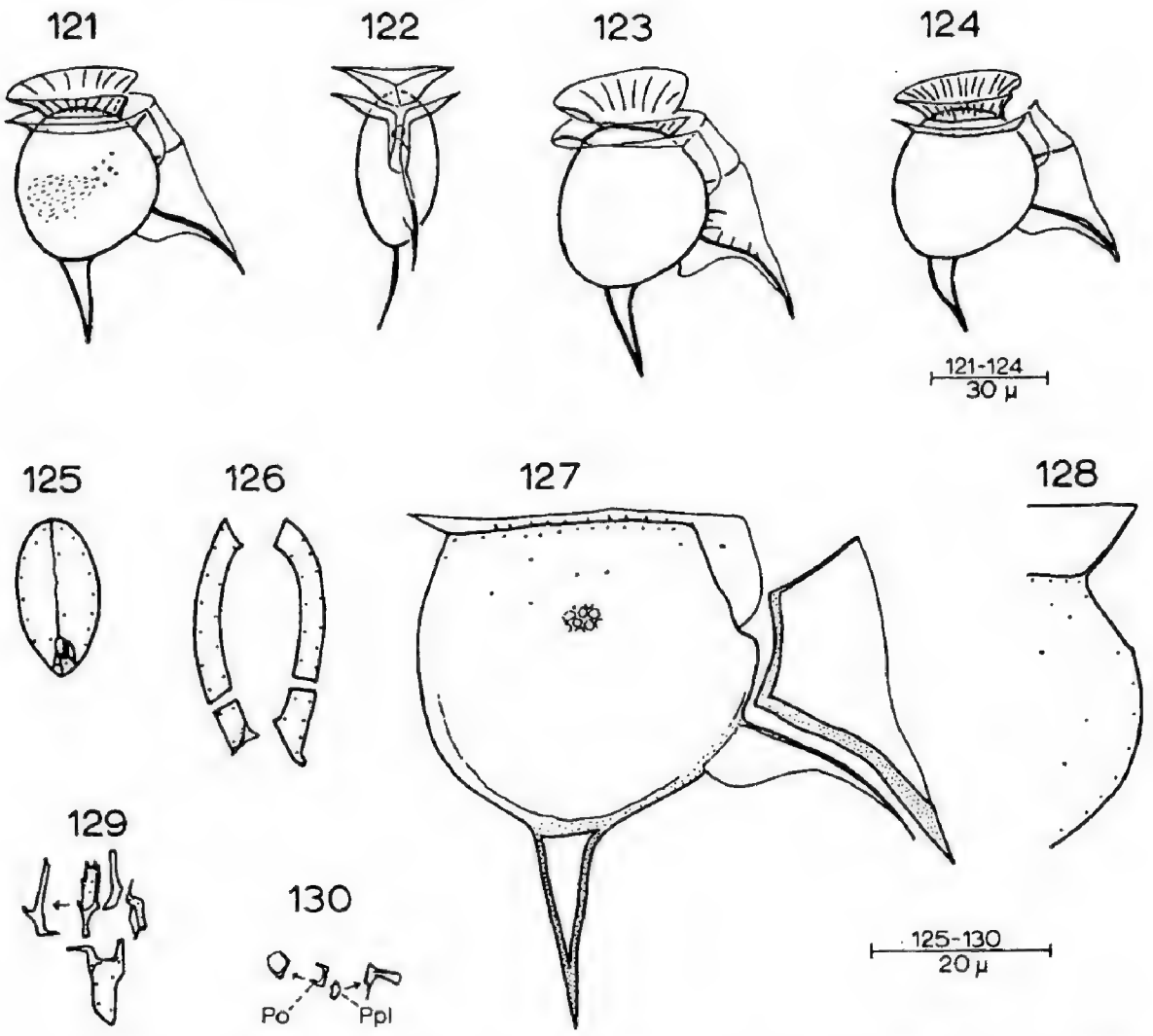
Figures 121–130

Dinophysis uracantha Stein 1883: pl. 20, figs. 22, 23.—?Jörgensen 1923: 32, fig. 42.—Kofoid and Skogsberg 1928: 273, fig. 35.—?Rampi 1940: 263, fig. 38.—Wood 1954: 200, fig. 48.—non Silva 1956: 356, pl. 3, fig. 5.

non *Dinophysis uracantha* Stein (var. *mediterranea*) Jörgensen 1923: 32, fig. 43.—Silva 1958: 22, pl. 1, fig. 4.—Halim 1960: pl. 2, fig. 3.

General

The rather small individuals representing this species are asymmetrically ellipsoidal in lateral view, rounded symmetrically anteriorly and asymmetrically posteriorly, and deepest near the middle. The length to depth ratio is 1.06–1.08:1. The longitudinal axis is deflected 6–11° dorsally.



FIGS. 121–130. *Dinophysis uracantha.* 121 and 122, an individual from sample BN-15; 123, another individual from sample BN-15; 124, an individual from sample BN-16; 122 is in ventral view, the others are in right lateral view. 125–130, thecal plates: 125, epitheca with omission of the anterior cingular list, from individual represented in Fig. 124; 126, cingular plates; 127, H_3 and H_4; 128, ventral portion of H_2 as seen from within; 129, sulcal plates; 130, Po and Ppl. 126–128 are from the individual represented in Figs. 121 and 122; 129 and 130 are from the individual represented in Fig. 123.

The epitheca is 0.47–0.50 as deep as the hypotheca, moderately convexed, highest near the middle, and distinctly below the distal margin of the anterior cingular list. The cingulum is slightly convexed, its width is 1.33–2.00 the height of the epitheca. It is quite uniform in width throughout its dorsoventral length. The posterior cingular list is 0.13–0.14 the body length from the apex. The hypotheca is asymmetrical, its dorsal margin is moderately convexed. The ventral margin is more convexed and tends to be flattened anteriorly and/or posteriorly. The posterior end is asymmetrically convexed. In ventral view the body is narrowly subelliptical with rather symmetrical sides and widest near the middle. The posterior end is slightly more narrowly rounded than the anterior. The length to width ratio is 1.73–1.81:1; the depth of the cingulum to the transdiameter is 1.65–1.67:1.

The anterior cingular list is 2.44–3.00 the width of the cingulum; the posterior is 0.58–0.75 the width of the anterior. The anterior is inclined anteriorly 22–25°, the posterior is nearly horizontal to an anterior inclination of 26.5°. Simple, complete and incomplete radial ribs of weak to moderate strength are present on the

anterior list; under oil immersion tenuous radial ribs may be seen in the posterior cingular list. The left sulcal list is 0.63–0.74 the body length and two to three times wider posteriorly than anteriorly. The ventral margin is irregularly oblique with straight to sigmoid portions; the posterior is quite sigmoid, in one individual forming a small lobe rather suggestive of *D. swezyi*. An acute angle of ca. 25–35° is formed at R_3. R_2 is 0.23–0.29, R_3 0.75–0.83 the greatest body depth. The ribs of this list are moderately to well developed. R_1 is straight, R_2 is nearly so to slightly sigmoid or concaved forward, R_3 is straight proximally and then bends posteriorly or it is gently to moderately concaved posteriorly. The latter rib is inclined 31–39° posteriorly. The left sulcal list is smooth or has a few short, irregular ribs. The right sulcal list ends behind R_2, it is subuniform in width throughout the greater part of its length, rounded posteriorly and smooth. The posterior sail is somewhat dorsal to the midline and inclined 7–18° ventrally. Its base is 0.33–0.43 its length. This list has marginal ribs which are slightly concaved to sigmoid. Its length is 0.58–0.62 the body depth.

Thecal Plates

The thecal wall is moderately thick, individual plates are of moderate strength. The epitheca is subelliptical in apical view. Each dorsal epithecal plate is straight or has a gentle undulation along the sagittal suture. The ventral notch is decidedly larger in the left plate than in the right. These plates are smooth and each has a row of pores near the lateral margin and one or two near the sagittal margin.

The pore plate is subrectangular to elliptical. It forms the right dorsal portion of the apical pore. In apical view, the left margin appears thickened as if a list were present, this was not confirmed however.

The pore platelet is subequal in size to Po and somewhat less regularly shaped. It appears to form the left margin of the apical pore. The presence of a list on this platelet was confirmed in one individual. Ppl touches E_1 dextroventrally, E_2 to the left and dorsally and Po to the right.

The cingular plates are smooth. C_1 is 1.42–1.75 the length of C_4, it broadens ventrally, slightly more posteroventrally where it ends in a small finger-like projection. The ventral margin is oblique. C_4 is subtrapezoidal and has a small ventral list which extends somewhat along the anterior margin. C_1 has two pores near the anterior border and three to four near the posterior, C_4 has one and two pores respectively.

The dorsal hypothecal plates appear smooth along the sagittal suture or have small, rounded denticles. These plates possess a small, irregular polygonal reticulation which extends to near the margins. Under low magnification this reticulation appears as closely knit poroids. The ventral hypothecal plates together are 0.62–0.66 the length of the hypotheca. H_4 is 1.43–1.55 the length of H_1 which is subequal to both C_1 and S_p. A row of three to four pores is present on H_1, five to six on H_4.

The sulcus is 0.79–0.83 the length of H_1 and H_4 together. It extends to 0.31–0.38 of the way down H_4. The anterior sulcal plate is narrow and elongate and is slightly sigmoid. The left sulcal plate in one instance was observed to possess a

small narrow list. One pore may be present in S_s. The right sulcal plate has an outward directed process at the base of the posterior extension. This may help support a small list along the right margin of S_d. There are two pores present.

The posterior sulcal plate is subequal to C_1 and H_1 and 0.22–0.24 the body length. The left margin lacks denticles. The anterior half of this plate is somewhat broader than the posterior due to a "shoulder" on the left and sometimes on the right margin. The posterior margin is oblique. There are three pores near the left margin and two to three near the right.

Dimensions

Body length, 38–42; total length, 57–66; epithecal depth, 17–19; hypothecal depth, 36–39; transdiameter, 15–17; body width, 21–24; maximum width of the left sulcal list, 23–27; R_1–R_2 9–10(12–15); R_2–R_3 12–15(33.5–39); R_3–PS 24–25.5(42).

Three specimens were measured and three examined for their plate morphology.

Variations

On the whole the individuals representing this species are quite similar. The most obvious variations are in the shape of the posterior sail and the left sulcal list—particularly its posterior margin. Also of interest is the presence of a list on the left sulcal plate of one individual, a character not seen in the other species of this study.

The individuals examined in this study fall within the variations presented by Kofoid and Skogsberg (1928). The present study illustrates *Dinophysis uracantha* in ventral view and gives an analysis of the thecal plates for the first time.

DISCUSSION

Systematics

The main objective of these plate analyses is to critically examine the thecal morphology of representatives of the *Dinophysis* "hastata" group present in the Gulf of Mexico. This presentation provides additional information toward unraveling the confusion in dinoflagellate taxonomy and more specifically in the "hastata" group. It also may have added some confusion by the disclosure of an additional plate which was always present in the epitheca of the species examined. The plate formula found here is therefore: 6 E (epithecal) (previously 5 E), 4 C (cingular), 4 H (hypothecal), and 4 S (sulcal). It is tempting to say that this formula is true for *Dinophysis* as a whole, but much effort in examining other representatives is necessary to confirm this. The type species, *D. acuta* Ehrenberg, has priority in establishing the plate formula for *Dinophysis*.

A second objective of this study is to attempt to ascertain from field samples whether there are definitive morphological criteria by which the species in this group can be delimited. It must be said that there is no one character or set of characters which can be used to delineate a given species. What suffices for one will not for another. Analyses of thecal plates does not always give evidence for separation of species. For example, *Dinophysis doryphora* and *D. paulseni* have

very similar plates, these species must still be separated on the basis of size and body shape. On the other hand, such things as the relative sizes and shapes of C_1 versus C_4, H_1 versus H_4, and S_p are helpful in distinguishing certain species. In this study for example, *D. balechi* can be separated from *D. hastata* on the basis of the relative length of H_1 versus H_4 and on the shape and relative length of S_p. As mentioned under *Remarks* in the discussion of *D. hastata* it is believed that future studies will result in descriptions of new species on the basis of thecal analyses.

In addition to the general morphology of the whole organism, which should include examination in ventral view, the following are considered here to be most important: the total plate pattern and formula; the relative sizes and shapes of C_1 versus C_4 and H_1 versus H_4; and the relative size and shape of S_p. The thecal lists, on which considerable emphasis was placed in the past, are believed to be of secondary importance because of their greater variation.

Distribution

Vertical distribution, as related to vertical migration, of dinoflagellates has been inferred by Hasle (1950, 1954a) who reviewed much of the earlier work; more recent literature is reviewed by Eppley *et al.* (1968). Vertical distribution *per se* is discussed by Hasle (1945b), Smayda (1958), Wood (1965) and Bernhard and Rampi (1967); additional references to earlier work are found in these papers. There is little literature on the vertical distribution of the species discussed in the present paper. Though found in surface waters, the genus *Dinophysis* as a whole seems to have its optimum habitat in deeper levels (Kofoid and Skogsberg 1928: 220). Kofoid and Skogsberg point out that the vertical distribution is little known and mostly inferred from vertical hauls. Karsten (according to Kofoid and Skogsberg) records *Dinophysis* (*Phalacroma*) *doryphora*, *D. hastata*, and *D. uracantha* in catches made with closing nets. The first species was recorded in the following depth ranges: 1600–1400 m; 1000–800 m; 420–350 m; 120–105 m; 105–88 m; and 63–46 m. *D. hastata* and *D. uracantha* were both taken in a haul from 80 to 60 m. Gaarder (1954, Tables 1–5) lists several members of the "hastata" group with depth ranges. *D. hastata* was taken from 210 to 140 m by Halim (1960: 229). Balech (1967a: 289) indicates that *D. hastata*, *D. schuetti*, and probably *D. odiosa* are shade species. The second species (*D. schütti*) is listed as a shade species by Halim (1967: 703). According to Kofoid and Skogsberg (1928: 53 and 219), most species of *Dinophysis* are limited to tropical to warm-temperate waters.

The data in Table 2 imply some degree of vertical distribution in these species. *Dinophysis doryphora*, *D. hastata*, *D. pusilla* and *D. schuetti* are present from the surface to at least 110–120 m. *D. paulseni* appears to be only at depths greater than 50 m, and *D. uracantha* at greater than 100 m. *D. circumsuta* and *D. swezyi* (one individual of each) were taken in the 110–120 m range. *D. odiosa* (one individual) and *D. balechi* were found only in relatively shallow (upper 15 m) water. These data suggest that *D. circumsuta*, *D. paulseni*, *D. swezyi*, and *D. uracantha* are "shade" species; *D. balechi* and *D. odiosa* seem to prefer higher light intensities.

Additional Note

In recent communications with Professor Enrique Balech it was learned that he has two publications "in press" in which he reveals an "extra" epithecal plate in several species of *Dinophysis* (none of which are discussed in this paper). He is in accord with the analyses made here but calls the "new" plate an apical plate (A_1) rather than pore platelet (Ppl). The term apical plate may be useful in order to maintain a continuity with other genera which have two or more such plates associated with the pore plate.

Concerning the difference in interpretation of the sulcal region of *D. pusilla* (see *Variations* under *D. pusilla*), Professor Balech points out that S_s sometimes overlaps the end of S_a making S_a appear shorter than it really is. Thus, S_a probably always is in communication with the flagellar pore.

ACKNOWLEDGMENTS

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A CHECKLIST OF THE MOLLUSKS OF SEVEN AND ONE-HALF FATHOM REEF, NORTHWESTERN GULF OF MEXICO[1]

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ABSTRACT

One hundred and sixty-nine species of mollusks (55 alive) were collected from Seven and One-Half Fathom Reef, a small sedimentary rock outcrop located in the shallow waters on the continental shelf of the northwestern Gulf of Mexico. The mollusks collected consisted of 108 Gastropoda, 3 Scaphopoda, 57 Pelecypoda and 1 Cephalopoda. Thirty seven had not been previously reported as occurring along the Texas coast. SCUBA, a new approach to collecting the fauna of the northwestern gulf, was employed to sample the mollusks and proved to be very successful.

INTRODUCTION

Hedgepeth (1953) states that the estuarine and neritic waters of the northern Gulf of Mexico, especially along the coast of Texas and Louisiana, are characterized by broad ranges of environmental factors that provide favorable conditions for temperate organisms in the winter and tropical organisms in the summer. "The fauna is a mixture of temperate Atlantic and tropical Caribbean elements, with a very low endemic component." Ladd (1952), Hedgepeth (1953) and Hildebrand (1954) sampled the bottom fauna of this area using dredges and trawls. Most of their collecting, however, was from commercial shrimp trawlers or school-owned boats which must avoid banks and reefs to prevent entanglement of their equipment.

Parker and Curray (1956), using a dredge, and Moore (1958b), wading and snorkling, sampled bank and reef fauna of the western Gulf of Mexico. Although these techniques produced species new to the western Gulf, they could not exhaustively examine the different habitats on and adjacent to the reefs. SCUBA has provided a new and efficient technique to accomplish this purpose.

DESCRIPTION OF STUDY AREA

Seven and One-Half Fathom Reef is a small topographic prominence located on the continental shelf of the northwestern Gulf of Mexico, approximately

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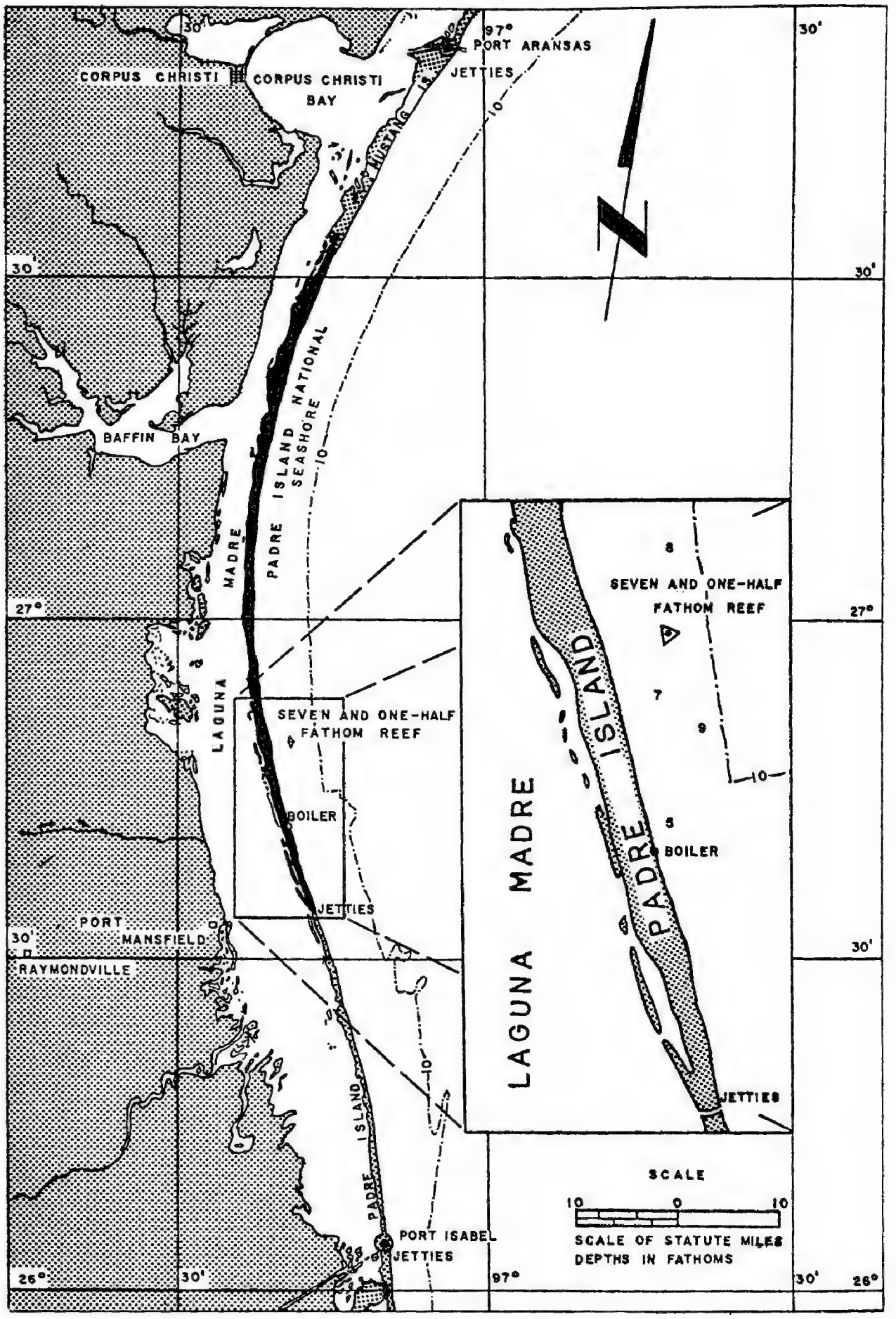

FIG. 1. The South Texas coast from Port Aransas to Port Isabel, showing the approximate location of Seven and One-Half Fathom Reef.

26°51′N, 97°18′W. The reef is 74 kilometers south of the northern entrance to Padre Island National Seashore and 3.2 kilometers offshore from Padre Island (Fig. 1). The bottom surrounding the reef is 14.0 meters deep with a noticeable amount of scouring evident on either side. The beach side of the reef has been

deeply scoured while the scour on the gulf-side is not as evident because of the buildup of organic material and mud.

The reef is an elongate sedimentary rock structure composed of a silty quartz sandstone that is partially cemented with calcium carbonate. There are 4 distinct rises which are oriented at an approximate 45° angle to Padre Island. The second rise from the south, with a relief of 5.4 meters, is greater in all dimensions than the other 3 rises and was chosen as the main area of study.

Beginning at the southern rise, the reef extends due northwest to the end of the third rise, approximately 250 meters distance, and then makes a 10° bend to the west northwest and extends another 100 meters to the end of the fourth rise. Numerous small outcrops of rock of 1 to 5 meters surface area dot the fringes of the reef.

The general topography is rough, with numerous crevices and small caverns. The sides vary from steep, precipitous cliffs, dotted with pockets, to even gentle slopes. Boring mollusks and other organisms have extensively attacked the structure, mostly in areas above 10 meters, leaving a riddled surface. Rock fragments of varying size present in the bottom of most crevices demonstrate the continual breakage of the structure. Sponges, hydroids, bryzoans and algae have encrusted the upper levels of the reef to such an extent that bare rock is scarcely visible.

Mammal teeth and bones found in the crevices (Tunnell and Causey 1969) and freshwater snails in the rock indicate a terrestrial origin of the reef.

Water salinity around the reef during the study varied at the surface from 27.8 ppt in late September 1968 to 35.8 ppt during late July and August 1968; at the bottom from 28.1 ppt in late September 1968 to 35.9 ppt during late August 1969. Temperatures ranged from a low of 13.2 C at the surface during late January 1968 to a high of 30.1 C during mid August 1968.

Visibility ranged from approximately 3–0 meters through a surface-to-bottom column of water during early February of 1969 to 25–5 meters during early August 1968. The top of the reef could be seen from the boat during this period of approximately one week. The visibility was usually greater in the surface waters than in lower levels. However, clear layers were sometimes observed between the surface and bottom waters or on the bottom only.

The range of average visibility (visual observation only) was 8–10 meters on the surface of the water, 5–7 meters on top of the reef and 0–3 around the bottom from May to late October. Murky water usually prevailed during the late fall, winter and early spring months. However, when the winds calmed during this period and the barometric pressure was high the water cleared. Visibility of approximately 15 meters was found during mid February 1969 at the top and bottom of the reef.

The water color varied from a deep blue during the summer months to a deep emerald green during the fall and winter months.

METHODS AND MATERIALS

Diving with SCUBA was employed to sample and observe the mollusks since it is the only feasible way to adequately sample a hard rock reef. The use of SCUBA also allowed the researcher to observe the animals and collect life history data in their natural habitat.

Eighty 72 cubic inch SCUBA tanks (averaging 50 minutes per tank) were used in collecting and observing the mollusks of the reef from 11 April 1968 to 8 June 1969.

Trips were made to the study area (via four-wheel drive vehicles down Padre Island then by small boat through the surf to the reef offshore) at any time during the duration of the study when weather and water conditions would permit diving. More trips were made during July and August because optimum diving conditions prevailed.

Three sampling methods were utilized for collecting 4 different groups of mollusks: mud samples for collecting micromollusks; rock samples for boring and attached species; and random sampling for motile macro-mollusks.

Mud samples—Mud samples were collected in gallon jars from the crevices and around the base of the reef. The samples were returned to the laboratory, washed in a 707 micron U. S. Standard Sieve and examined for mollusks.

Rock samples—Rocks were collected from all portions of the reef, placed in barrels of 10% formalin solution and returned to the laboratory where they were broken to pieces with a hammer and chisel and examined for mollusks.

Random sampling—In this method most of the surface of the reef was examined *in situ* by turning over rocks and looking in crevices and holes. Sponges, hydroids and algae were collected and later examined for small mollusks in the laboratory. The collected mollusks were returned to the laboratory alive or in a 10% formalin solution.

Mollusks from all sampling methods were identified using the most recent taxonomic keys, published articles and books for this area. Works most frequently used were were Clench (1942–68) Abbott (1954), Perry and Schwengle (1955), Warmke and Abbott (1961) and Chaney (unpublished keys). Some doubtful identifications were submitted to qualified authorities for confirmation and others were identified only to genus.

At least 1 individual of those species collected alive, except some nudibranches, was placed in the Texas A&I Mollusk Collection. Fresh and old shells in good condition were also placed in the collection. Single valves of pelecypods and worn gastropod shells were not placed in the collection, but are listed in the checklist.

CHECKLIST

Approximately 450 species of mollusks have been listed by various authors as occurring in Texas coastal waters. Pulley (1952) compiled a resumé of all marine species reported in previous works and included notes on their occurrence from his own observations. Moore (1958a, 1964) has confirmed some doubtful occurrences and reported species that were not previously listed.

The following is a list of 169 species of mollusks collected from Seven and One-Half Fathom Reef: 108 Gastropoda, 3 Scaphododa, 57 Pelecypoda and 1 Cephalopoda. Fifty-five species, collected alive, and 18 others that had recently died or found in large numbers were considered as reef residents. Others, such as *Tegula fasciata* (Born), *Modulus modulus* (Linné) and *Crassostrea virginica* (Gmelin) were represented by old worn shells (probably fossils) and probably are not living anywhere in the vicinity of the reef, since nowadays they are usually found in bays.

Thirty seven of the species collected, such as *Circulus* sp., *Vanikoro* sp., *Caecum clava* de Folin, *C. ryssotitum* de Folin and *Bursa cubaniana* d'Orbigny, have their reported centers of population in the western Atlantic, West Indies or Caribbean and have not been reported from the Texas coast or some even from the Gulf of Mexico. Probably the main reason is that the SCUBA technique has not been applied in this area.

Five species of nudibranchs were collected but have been omitted from the list pending definite identification from E. Marcus in Brazil.

The classification is the same as that used by Moore (1961), which is essentially the same as that employed by Morton (1958).

Systematic List—Mollusks of Seven and One-Half Fathom Reef

(Asterisk indicates species not previously reported as occurring along the Texas coast, A indicates collected alive and D indicates collected dead.)

Class Gastropoda

Subclass Prosobranchia	
Order Archaeogastropoda	
Family Fissurellidae	
Diodora cayenensis (Lamarck)	A
Family Trochidae	
Tegula fasciata (Born)	D
Calliostoma euglyptum (A. Adams)	A
Order Mesogastropoda	
Family Rissoidae	
cf. *Cingula sandersoni* Verrill	D
Rissoina chesneli (Michaud)	D
R. decussata (Montagu)	D*
Family Vitrinellidae	
Vitrinella helicoidea C. B. Adams	D
V. floridana Pilsbry and McGinty	D
Teinostoma biscaynense Pilsbry and McGinty	D
Episcynia inornata (d'Orbigny)	D
Solariorbis infracarinate (Gabb)	D
Cyclostremiscus pentagonus (Gabb)	D
C. jeannae Pilsbry and McGinty	D*
Parviturboides interruptus (C. B. Adams)	D
Macromphalina palmalitoris Pilsbry and McGinty	D
Circulus sp.	D*
Vanikoro sp.	D*
Family Turritellidae	
Vermicularia spirata Philippi	A
Family Architectonicidae	
Heliacus bisulcatus d'Orbigny	A*
Architectonica nobilis (Röding)	D
Family Caecidae	
Caecum pulchellum Stimpson	D
C. cooperi S. Smith	D*
C. clava de Folin	D*
C. cf. *glabrum* (Montagu)	D*
C. ryssotitum de Folin	D*
Family Modulidae	
Modulus modulus (Linné)	D
Family Cerithiidae	
Alabina cerithidioides (Dall)	D*

Seila adamsi (H. C. Lea)	A
Family Litiopidae	
Litiopa melanostoma Rang	D
Family Cerithiopsidae	
Alaba incerta (d'Orbigny)	D*
Cerithiopsis greeni (C. B. Adams)	D
C. emersoni (C. B. Adams)	A*
Family Triphoridae	
Triphora nigrocincta (C. B. Adams)	D
Family Epitoniidae	
Amaea mitchelli (Dall)	D
Epitonium angulatum (Say)	D
E. apiculatum Dall	D*
E. candeanum (d'Orbigny)	D*
E. multistriatum (Say)	D
E. sp.	D
Family Eulimidae	
Balcis conoidea (Kurtz and Stimpson)	D
B. intermedia (Cantraine)	D*
B. bilineata (Alder)	D
Eulima bifasciata d'Orbigny	D*
Niso interrupta (Sowerby)	D
Family Calyptraeidae	
Crepidula fornicata (Linné)	A
Family Strombidae	
Strombus alatus Gmelin	D
Family Cypraeidae	
Cypraea cervus Linné	A*
Family Ovulidae	
Neosimnia acicularis (Lamarck)	A*
Cyphoma mcgintyi Pilsbry	A*
Family Naticidae	
Neverita duplicatus (Say)	D
Sinum perspectivum (Say)	D
Tectonatica pusilla (Say)	A
Family Cassididae	
Phalium granulatum (Born)	D
Family Cymatiidae	
Cymatium pileare (Linné)	D
C. parthenopeum (von Salis)	A
Distorsio clathrata (Lamarck)	D
Family Bursidae	
Bursa cubaniana d'Orbigny	A*
Order Neogastropoda	
Family Muricidae	
Murex pomum Gmelin	A

M. fulvescens (Sowerby)	A
M. florifer Reeve	D*
Morula nodulosa (C. B. Adams)	A
Thais haemastoma (Linné)	A
Family Columbellidae	
Pyrene iontha (Ravenel)	D*
Anachis avara (Say)	A
A. obesa (C. B. Adams)	D
A. translirata (Ravenel)	A
A. sp.	D
Mitrella lunata (Say)	D
Family Buccinidae	
Pisania tinctus (Conrad)	A
Cantharus cancellaris (Conrad)	A
Family Melongenidae	
Busycon spiratum (Lamarck)	D
Family Nassariidae	
Nassarius albus (Say)	A
N. acutus (Say)	D
Family Fasciolariidae	
Fasciolaria hunteria (Perry)	A
Pleuroploca gigantea (Kiener)	A
Family Olividae	
Oliva sayana Ravenel	D
Olivella minuta (Link)	D*
O. mutica (Say)	A
Family Cancellariidae	
Cancellaria reticulata (Linné)	D
Family Terebridae	
Terebra cinerea Born	D
T. dislocata Say	D
Family Turridae	
Crassispira cf. *harfordiana* Reeve	A*
Mangelia sp.	D
M. sp.	D
M. sp.	D
Kurtziella cerinella (Dall)	D
Rubellatoma diomeda Bartsch and Rehder	D*
Subclass Opisthobranchia	
Order Cephalaspidea	
Family Acteonidae	
Acteon punctostriatus (C. B. Adams)	D
Family Bullidae	
Bulla striata Bruguière	D

Family Atyidae	
Haminoea sp.	D
Family Retusidae	
Retusa canaliculata (Say)	D
Pyrunculus caelatus Bush	D*
Volvulella persimilis (Mörch)	D*
Family Acteocinidae	
Cylichna bidentata (d'Orbigny)	D
Family Pyramidellidae	
Pyramidella candida Mörch	D
P. crenulata (Holmes)	D
Turbonilla cf. *portoricana* Dall and Stimpson	D*
T. sp.	D
T. sp.	D
T. sp.	D
Odostomia seminuda (C. B. Adams)	D
O. sp.	D
O. sp.	D
Order Anaspidea	
Family Aplysiidae	
Aplysia willcoxi (Heilprin)	A*
A. floridensis (Pilsbry)	A
Order Thecosomata	
Family Cavolinidae	
Cavolina longirostris (LeSeur)	D*
Cresis acicula (Rang)	D
Order Nudibranchia	
Family Scyllaeidae	
Scyllaea pelagica Linné	A
Class Scaphopoda	
Family Siphonodentaliidae	
Cadulus carolinensis Bush	D*
Family Dentaliidae	
Dentalium texasianum Philippi	D
D. eboreum Conrad	D
Class Pelecypoda	
Order Protobranchia	
Family Nuculanidae	
Nuculana acuta (Conrad)	D
N. concentrica (Say)	D
Order Taxodonta	
Family Arcidae	
Arca zebra (Swainson)	A

A. imbricata Bruguière	A
Barbatia candida (Helbling)	A
B. domingensis (Lamarck)	A
Anadara transversa (Say)	A
Noetia ponderosa (Say)	A
Order Anisomyaria	
Family Mytilidae	
Gregariella coralliophaga (Gmelin)	A
Lioberus castaneus (Say)	D
Lithophaga aristata (Dillwyn)	A
L. bisulcata (d'Orbigny)	A
Family Pinnidae	
Atrina rigida (Solander)	A
A. serrata (Sowerby)	D
Family Pteriidae	
Pteria colymbus (Röding)	A
Family Isognomonidae	
Isognomon radiatus (Anton)	A
Family Ostreidae	
Ostrea equestris Say	A
Crassostrea virginica (Gmelin)	D
Family Pectinidae	
Pecten raveneli Dall	D*
Lyropecten nodosus (Linné)	A
Aequipecten muscosus (Wood)	A*
Family Spondylidae	
Spondylus americanus Hermann	A
Family Plicatulidea	
Plicatula gibbosa Lamarck	D
Family Limidae	
Lima pellucida C. B. Adams	A
Family Anomiidae	
Anomia simplex d'Orbigny	D
Pododesmus rudis (Broderip)	A
Order Heterodonta	
Family Crassatellidae	
Crassinella lunulata (Conrad)	D
Family Carditidae	
Cardita floridana (Conrad)	D
Family Diplodontidae	
Diplodonta punctata (Say)	A
Family Lucinidae	
Lucina multilineata (Tuomey and Holmes)	D
L. amiantus (Dall)	D
Divaricella quadrisulcata (d'Orbigny)	D*

Family Chamidae	
Chama congregata Conrad	A
Pseudochama radians (Lamarck)	A
Echinochama arcinella (Linné)	D
Family Cardiidae	
Trachycardium muricatum (Linné)	A
Laevicardium sp.	D
Dinocardium robustum (Solander)	D
Family Veneridae	
Chione grus (Holmes)	A
C. clenchi Pulley	D
Dosinia elegans (Conrad)	D
Mercenaria campechiensis (Gmelin)	D
Gouldia cerina (C. B. Adams)	D
Family Petricolidae	
Rupellaria typica (Jonas)	A
Family Tellinidae	
Tellina alternata Say	D
T. versicolor DeKay	D
T. sp.	D
Quadrans lintea (Conrad)	D
Family Semelidae	
Abra aequalis (Say)	D
Semele proficua (Pulteney)	D
S. purpurascens (Gmelin)	D
Order Adapedonta	
Family Mactridae	
Mulinia lateralis (Say)	D
Family Corbulidae	
Notocorbula opercultata (Philippi)	D*
Corbula contracta Say	D
C. sp.	D
Family Gastrochaenidae	
Gastrochaena hians Gmelin	D*
Order Anomalodesmata	
Family Lyonsiidae	
Lyonsia beana d'Orbigny	A*
Class Cephalopoda	
Subclass Coleidea	
Order Octopoda	
Family Octopodidae	
Octopus vulgaris Lamarck	A

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FIELD AND CULTURAL STUDIES OF *ULVA* AND *ENTEROMORPHA* IN THE VICINITY OF PORT ARANSAS, TEXAS[1]

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ABSTRACT

Field and cultural investigations were conducted on eight species of Ulvaceae occuring on the Texas coast: *Ulva lactuca, U. fasciata, Enteromorpha clathrata, E. salina, E. lingulata, E. prolifera, E. ramulosa,* and *E. flexuosa.* Keys and descriptions based on a synthesis of information from field specimens and a literature survey are presented. Reproductive history was determined for each species in culture. Three types of reproduction were noted in these isolates: (1) an alternation between unisexual gametophytes and sporophytes; (2) reproduction of a single morphological phase by quadriflagellate zoospores; and (3) an alternation between generations sequentially producing bi- and quadriflagellate zoospores. Isolates of all species were grown under uniform environmental conditions to determine the constancy of specific morphological characters. Frond shape, degree of branching, and cellular dimensions were observed to be fairly constant and in close agreement with data from field specimens. A tendency was noted for certain species to be sexually dimorphic in culture, the male gametophytes being larger and more highly branched than the females. Cytological investigations revealed an alternation of haploid and diploid phases in *Ulva fasciata* and *Enteromorpha salina.* A haploid number of ten chromosomes was determined for all species. Attempts at obtaining interspecific and intergeneric hybrids in sexually reproducing *Ulva* and *Enteromorpha* species failed. Evidence for interspecific sterility is discussed and explanations given for the spontaneous appearance of a new germling type among the putative hybrids.

INTRODUCTION

The Ulvaceae are widespread, thriving in most marine habitats that provide solid anchorage in the intertidal zone. Most species are able to exist in a wide range of salinities, and are present in bays, estuaries, and inland bodies of salt water. *Enteromorpha* can often be found in salt marshes and has been collected occasionally in inland bodies of freshwater (Taft 1964).

Ulvaceae are separated from other ulotrichalean algae by their production of

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a hollow parenchymatous thallus (Bliding 1963). In *Ulva*, the tubular thallus becomes compressed and the walls grow together forming the characteristic distromatic blade, while in *Enteromorpha*, the tubular construction is maintained (Bliding 1963).

Most Ulvaceae have an alternation of isomorphic gametophytic and sporophytic generations (Hartman 1929; Føyn 1929, 1934; Ramanathan 1936; Bliding 1963). Meiosis has been reported to occur at the first nuclear division in the formation of zoospores in *Enteromorpha* (Ramanathan 1936, 1939) and in *Ulva* (Føyn 1934). There are some exceptions to this type of life cycle. *Enteromorpha linza* reproduces only asexually by bi- and quadriflagellate zoospores (Bliding 1939; Dangeard 1961a). *Enteromorpha intestinalis*, in addition to races with the regular alternation, has those which produce only zoospores (Bliding 1944).

The Ulvaceae includes three genera: *Ulva*, *Ulvaria*, and *Enteromorpha* (Bliding 1963, 1968). This paper presents the results of field and cultural investigations of the two genera on the Texas Gulf Coast in the vicinity of Port Aransas, namely, *Ulva* and *Enteromorpha*. Both genera, but especially *Enteromorpha*, are notorious for their baffling range of morphological characters. Morphological characters such as frond branching, cell size, shape and arrangement proved inadequate to delimit the local species satisfactorily. Consequently, living material representing the different species types was cultured to provide otherwise unavailable information about the type of life history, production and behavior of swarmers, and the morphology of germlings. This combination of information made it possible to delimit the species investigated. Finally, the resulting cultures were given specific designations and used for comparative studies.

MATERIALS AND METHODS

Ulva and *Enteromorpha* species were collected periodically from the Port Aransas, Texas, southwest jetty on the Gulf of Mexico and sites near Fulton and Rockport on Aransas Bay from March, 1967, through March, 1969. Fifteen separate collections were made in addition to a six-week intensive study during the summer of 1967 at the Institute of Marine Science at Pt. Aransas. Information concerning growth and abundance, as well as substrate, exposure, and position relative to tidal levels was recorded for each species.

Cultures were established by collecting swarmers from sporulating material and transferring them to Petri dishes of sterile seawater. Cultures were placed in 50-ml Erlenmeyer flasks with cotton plugs and filled with 40-ml of medium. The flasks were illuminated with 200 ft-c incident light from 40-W Ken-Rad "Cool White" fluorescent bulbs in a culture chamber maintained at 22 C with a 24-hr cycle of 12-hr light and 12-hr dark.

Various salt water media were used, including seawater enrichments and defined artificial seawater. Erdschrieber medium (Føyn 1934) was used initially, but failed to promote adequate growth. Artificial seawater media were then tried. Ott's (1965) modification of McClendon's artificial seawater (Sverdrup *et al* 1942) was found unsatisfactory and was enriched according to Haxo and Sweeney (Provasoli *et al* 1957) without much improvement. Jones' modified artificial seawater (Jones *et al* 1963) based on a substitution of artificial seawater enriched with von Stosch's salts as described by Nichols and Lissant (1967) was quite adequate. Another artificial seawater, ASP_2 (NTA), developed by Provasoli (1964) was equally good. Finally, von Stosch's enrichment of natural seawater as cited by Ott (1966) proved to be the most satisfactory medium and was utilized thereafter. This medium was prepared as follows:

One ml of each of the six stock solutions given below was added to 1 liter of natural seawater

which had been filtered through Whatman No. 1 filter paper. The final solution was then autoclaved at 15 psi for 25 min.

The micro-element stock solutions were prepared by dissolving the salts listed below in separate aliquots of 200 ml distilled water.

1. $NaNO_3$	8.5 g
2. $Na_2HPO_4 \cdot 12H_2O$	2.15 g
3. $FeSO_4 \cdot 7H_2O$	55.6 mg
4. $MnCl_2 \cdot 4H_2O$	3.9 mg
5. $Na_2EDTA \cdot 2H_2O$	0.74 g

The vitamins listed below were dissolved in a single aliquot of 200 ml distilled water.

6. biotin	0.2 mg
thiamin-HCl	40.0 mg
B_{12} solution (1000 ug/ml)	0.2 ml

OBSERVATIONS AND RESULTS

A. Field Studies

1. Previously Described Ulvacean Species in the Port Aransas Area.

Although a number of algal collections have been reported from the vicinity of Pt. Aransas (Taylor 1936, 1941; Smith 1938; Humm and Hildebrand 1962; Conover 1964), no general agreement exists on the specific delimitation of the Ulvaceae present (Table 1). A total of nine species has been recorded, but most workers have included only about half of these in their individual checklists.

There are several reasons for such a discrepancy. Most of the records were from sporadic collections and, consequently, species which are only present at certain times of the year were likely to have been overlooked. Other records are undoubtedly based upon collections made at only a few of the diverse habitats in the area and, therefore, omit species restricted to certain habitats. Finally, the state of the taxonomy of the Ulvaceae is such that specific identifications, especi-

TABLE 1

List of Ulvacean species collected in the vicinity of Port Aransas, Texas

Species	Taylor (1936)	Smith (1938)	Taylor (1941)	Humm & Hildebrand (1962)	Conover (1964)	Parker (1964)	Kapraun
Ulva lactuca	x	x	x	x	x		x
U. lactuca v. latissima	x				x		x
U. lactuca v. rigida				x	x		x
Ulva fasciata	x		x	x	x		x
Enteromorpha lingulata	x	x	x	x			x
Enteromorpha flexuosa		x	x	x	x		x
Enteromorpha prolifera		x	x		x		x
Enteromorpha salina						x	x
Enteromorpha clathrata				x	x		x
Enteromorpha plumosa		x	x		x		
Enteromorpha ramulosa							x
Enteromorpha intestinalis		x			x		

ally of members of the genus *Enteromorpha*, can be exceedingly difficult and uncertain.

Monthly collections were made over a period of two years from four distinct habitats. Of the nine species previously recorded, eight were collected during this investigation (Table 1). They are: *Ulva lactuca, U. fasciata, Entermorpha lingulata, E. flexuosa, E. prolifera, E. salina,* and *E. clathrata.* Both recorded varieties of *Ulva lactuca, U. lactuca* v. *latissima* and *U. lactuca* v. *rigida,* were also collected.

All of these species, except *E. salina,* had been recorded frequently enough by others to make their occurrence in this study probable. *Enteromorpha salina,* though reported only once before for Pt. Aransas (Parker 1964), has a distribution which includes the West Indies and Louisiana (Humm and Taylor 1961), Florida (Madsen and Nielsen 1950; Taylor 1960), and Mexico (Humm and Hildebrand 1962). Because of the proximity of the Texas coast to this established range it is not surprising that occasional individuals would be found at Pt. Aransas.

The remaining two species, *Enteromorpha plumosa* and *E. intestinalis,* are not reported by the writer. According to Collins (1903) and Taylor (1960), the range of *E. intestinalis* has a southerly limit off the coast of North Carolina, and reports from tropical areas should probably be interpreted as *E. flexuosa* and *E. lingulata.* Even though *E. intestinalis* had been previously recorded in Texas (Smith 1938, Conover 1964), this was not confirmed. In accordance with Taylor's opinion, *E. intestinalis*-like material was grouped by the writer with *E. flexuosa.* Information made available through cultural studies later confirmed the appropriateness of this decision.

Smilarly, the presence of *Enteromorpha plumosa* was not confirmed despite previous records by Smith (1938), Taylor (1941) and Conover (1964). Material was encountered which answered to the description of this species, but most specimens displayed a gradation of morphological characters between *E. clathrata* and *E. plumosa.* Apparently this is not an exceptional situation. Humm and Taylor (1961) included such dubious forms in *E. clathrata* in their study of the upper west coast of Florida. Bliding (1944) has presented evidence that the European varieties of *E. plumosa* and *E. clathrata* are synonymous. Because of the uncertain state of the taxonomy of these species and the lack of well-defined interspecific distinctions, *Enteromorpha plumosa*-like material encountered by this writer was grouped with *E. clathrata.*

Enteromorpha ramulosa, previously unrecorded for the Texas coast, has been identified. Taylor (1960) cites the West Indies and Florida as its geographical range. It is apparently common along the west coast of Florida where it has been reported by several investigators (Phillips 1960, Humm and Taylor 1961). Seemingly, this species, like *E. salina,* is found occasionally along the Texas coast.

There is a possibility that *Enteromorpha ramulosa* was included with *E. clathrata* by other workers, as the two species are similar. Collins (1903) recognized *E. clathrata* v. *ramulosa* as an intermediate between *E. clathrata* and *E. ramulosa.* Harvey (1858) reported that specimens of *E. clathrata* with short, spine-like ramuli are morphologically similar to *E. ramulosa.* Despite the simi-

larity of these two species, cultural studies provided characters which allowed a distinction to be made.

2. Keys and Descriptions to the Ulvaceae in the Vicinity of Pt. Aransas.

The following descriptions of and keys to the Ulvaceae of the Port Aransas area recognized in this investigattion are based primarily on the work of Taylor (1928, 1957, 1960). Publications used to a lesser extent include: Collins (1903, 1909), Carter (1926), Dawson (1944), Smith (1944), Tokida (1954), Humm and Caylor (1957), Humm and Taylor (1961) and Bliding (1963, 1968). The specific descriptions of these authors do not necessarily pertain to material from the American subtopics. Bliding's (1963, 1968) descriptions are based on specimens from Europe and those of Tokida (1954) on Japanese material. It is hoped that the recognized taxonomic characters used in this report for the identification of individual species are constant and uniform enough to be of value in recognizing specimens from any part of its range.

Besides these published sources, a detailed analysis of herbarium specimens prepared during the course of this investigation accounts for a large part of the specific descriptions. Consequently, these descriptions reflect the peculiarities of the Pt. Aransas flora.

Ulvaceae (Lamouroux) Rabenhorst

Plants consisting of a mono- or distromatic membrane or tube; simple or branched; attached by basal rhizoidal proliferations or free-floating; cells usually with a single parietal plastid with one to several pyrenoids and a single nucleus; sexual and asexual plants morphologically similar; asexual reproduction by bi- or quadriflagellate zoospores or parthenogenetic gametes which germinate directly; sexual reproduction by biflagellate gametes.

Ulva Linnaeus

Frond membranous, flat, consisting of two layers of cells separated by a gelatinous matrix; cells with a single plastid and generally one or two pyrenoids; uninucleate except for multinucleate holdfast cell extensions; asexual reproduction by four to eight quadriflagellate zoospores from each sporangial cell; sexual reproduction by eight to 16 slightly anisogamous biflagellate gametes, the individual plants usually unisexual.

Key to the Species of *Ulva* in the Vicinity of Port Aransas, Texas

1. Plants divided into narrow linear segments usually less than 1.5 cm wide ..... *Ulva fasciata*

1. Plants simple or with broad, irregular lobes 2

2. Blades irregular in outline, at first lanceolate but mostly exceeding

3.0 cm in width, rigid and dark green, 40–60 μ thick; cells in transverse section longer than wide ..... *Ulva lactuca* v. *rigida*

2. Blades broadly lobed, pale green and often with numerous perforations 1–5 cm wide, 30–45 μ thick; cells in transection nearly square or broader than long..... *Ulva lactuca* v. *latissima*[1]

Descriptions of the Texas Species of *Ulva*

Ulva fasciata Delile (Figs. 1, 2, 41–43)

Fronds 1–3 dm long, divided into contorted linear segments usually less than 1.5 cm wide, the margins smooth to crisped; cells of the central region taller than those of the margin; fronds about 50–80 μ thick; cells in surface view polyhedral or sometimes round, thick-walled, and irregularly arranged, 9–11 × 12–18 μ; cells in transverse section of the thallus longer than broad, 10–13 × 20–24 μ; pyrenoids 1–2.

This species differs from *Ulva lactuca* in the definite linear divisions of the frond which are lateral and sometimes dichotomous. These segments are typically less than 1.5 cm wide and 15 cm long, the maximum length approaching 50 cm. The margins are usually undulate and sometimes broadly serrate.

The distribution of this species is generally restritced to warm waters in tropical and warm temperate regions. It is common along the Atlantic coast from Florida north to North Carolina, throughout the Gulf of Mexico, and south to Brazil. It prefers wave-swept situations and forms dense mats on rocks and pilings which are continually buffeted by surf.

In this study, *Ulva fasciata* was found only on the southwest jetty at Port Aransas in wave-swept situations where it formed dense mats on the intertidal rocks. This species was most abundant during late spring and early summer, but could be found year around.

Ulva lactuca Linnaeus (Figs. 3, 4, 44, 45)

Fronds broadly lobed and undulate, sometimes slightly lanceolate toward the tips, to 2 dm long, delicately thin, 30–65 μ thick; cells in transverse section vary from horizontally to vertically elongate; cells in surface view distinctly and irregularly angular, compact, and in no definite arrangement.

This species is ubiquitous in marine waters and highly variable in form with two marked varieties in the study area.

var. *rigida* (C. Agardh) LeJolis

Fronds typically dark green and rigid, at first lanceolate but becoming broadly

[1] According to Papenfuss (1960), the type upon which this taxon is based is a species of *Laminaria*. Consequently, *Ulva* material matching the description of this variety should be reduced to synonymy under the variety *U. lactuca* var. *rigida* or referred to a new variety. Since two distinct types of *Ulva lactuca* were observed in this study, *U. lactuca* var. *rigida* and a type which would have previously been considered to be *U. lactuca* var. *latissima*, the material cannot be reduced to synonymy. Therefore, it seems best to distinguish the two types by temporarily retaining the incorrect, but familiar, varietal name until a valid variety is established.

lobed with occasional perforations; fronds 40–60 μ thick; the cells in transverse section vertically elongate, sometimes twice as long as wide, 20–22 × 14–16 μ; cells in surface view polygonal, 10–12 × 20–22 μ; pyrenoids 1–2.

This variety occurs in wave-swept situations and was found only on the southwest jetty at Port Aransas. Maximum growth was observed in late winter and early spring.

var. *latissima* (Linnaeus) DeCandolle

Fronds irregularly, broad lobed, often attached by an inconspicuous stipe, perforations of various sizes common; blades 30–45 μ thick; cells in transverse section more nearly square than in var. *rigida* but often horizontally elongate, 14–16 μ long and 20–22 μ long; cells in surface view polygonal, 14–16 by 18–20 μ; pyrenoids 1–2.

This variety occurs in protected situations such as tidal pools and bays. It was collected in sheltered situations in Aransas Bay and at Port Aransas. Maximum growth occurred during the spring.

Key to the Species of *Enteromorpha* in the Vicinity of Port Aransas, Texas

1. Frond simple or with few branches, to 15 cm tall and 1–1.5 cm wide, usually flattened or slightly inflated and contorted above ..... *E. flexuosa*
1. Frond with numerous branches 2
2. Branching chiefly near the base; branches 2–5 mm broad and ending in terete, colorless tips; cells rectangular and in clear longitudinal series ..... *E. lingulata*
2. Branching distributed throughout 3
3. Branching diffuse but of one order along the distinct main axis 4
3. Branching proliferous and of several orders; branches successively smaller than the main axis 5
4. Branches proliferous and similar to the distinct main axis which is 2–5 mm broad ..... *E. prolifera*
4. Branches abruptly smaller with the flattened main axis beset with numerous short, thorn-like branches 5–10 mm long ..... *E. salina*
5. Ultimate branches short, erect; cells subrectangular and irregularly placed ..... *E. ramulosa*
5. Ultimate branches elongate; cells distinctly rectangular and in longitudinal series ..... *E. clathrata*

Enteromorpha Link

Plants originating in a single series of cells which form a tubular frond with a monostromatic membrane; inflated or bulbous to capillary, simple or branched, tubular or with branches showing uniseriate filamentous tips; initially attached

by holdfasts formed by downgrowths from cells of the stalk-like portion; sometimes free-floating; cells usually closely placed and with a single plastid, a lateral plate more or less covering the outer or lateral face of the cell; generally with one to three pyrenoids and one nucleus; reproduction by zoospores and gametes produced in similar plants; all the cells of the frond, except the holdfast, capable of producing motile cells.

This is a large and complex genus with poorly marked interspecific distinctions and numerous intermediate forms. Although generally considered marine in habitat, representatives thrive in salt springs, brackish and estuarine waters, and occasionally in freshwater.

Enteromorpha clathrata (Roth) J. G. Agardh (Figs. 5, 6, 60–62)

Fronds to 3 dm long with axes 0.5–2.5 mm, filiform, soft, and often delicate with a system of branching of various orders; branches tapering from base to tip and almost always polysiphonous; cells rectangular, 11–13 × 20–23 μ, and in distinct longitudinal series; plastid smaller than cell face and occupying only part of the cell, giving a net-like appearance; pyrenoids 1–3.

This species differs markedly from all others, except *Enteromorpha plumosa*, in having a profuse system of branching of several orders with each set of branches smaller than the preceding. *Enteromorpha clathrata* differs from *E. plumosa* in that the former is typically more coarse, darker green, and lacks extensive monosiphonous branch tips. *Enteromorpha clathrata* cells have a small plastid, which results in a net-like appearance of the frond.

This species is found on the Atlantic coast of North America from Baffin Island to Florida and in the Gulf of Mexico. It prefers wave-swept situations but does occur in quiet waters where it becomes more delicate and superficially resembles *Enteromorpha plumosa.*

In this study, *Enteromorpha clathrata* was found on wave-swept intertidal rocks throughout Aransas Bay and at Port Aransas. This species was most abundant during the winter but could be found year around.

Enteromorpha ramulosa (Eng. Bot.) Hooker (Figs. 7, 8, 46–48)

Plants 6–10 cm tall, coarse and dark-green, tubular, stiff, and appearing bushy because of numerous short branches arising along the entire length of the main axis; branches of various sizes, usually tapering from the base to a slender tip of two to a few cells; cells in branches 8 × 13–15 μ, subrectangular, and in longitudinal series; cells in older parts 10–12 × 17–19 μ, polyhedral, thick-walled, irregularly arranged; pyrenoids 4–7.

This species superficially resembles *Enteromorpha salina*, with its thorn-like branches, and stouter varieties of *E. clathrata. Enteromorpha ramulosa* can generally be distinguished in the field by its coarse habit and by its intermediate degree of branching, having branches much longer than *E. salina*, but very seldom attaining the system of pronounced branching of several orders which is typical of *E. clathrata.*

Enteromorpha ramulosa is restricted to warmer waters and is found in the Bahamas and the Gulf of Mexico. This species was present on wave-swept inter-

tidal rocks throughout Aransas Bay but was most common in the southwest jetty at Port Aransas. It was most abundant during the winter months and became scarce in late summer.

Enteromorpha lingulata J. G. Agardh (Figs. 9, 10, 55, 56)

Plants tufted, composed of 4–8 branches which arise exclusively near the subsolid base; branches less than 7 cm tall and 1–3 mm wide; fronds gradually dilated, occasionally expanded to 5 or even 8 mm, and terete at the tips, which are colorless from massive sporulation in mature individuals; cells rectangular, 14–16 × 21–23 μ, in obvious longitudinal and transverse series throughout; cells thin-walled in surface view; pyrenoids 1–2.

Enteromorpha lingulata is limited to warm tropical and warm temperate waters from North Carolina to Florida, throughout the Gulf of Mexico, and south to Brazil. It is common on rocks and woodwork in moderately wave-swept sites near low tide level. This species was found at Port Aransas but was most common on intertidal shells in Aransas Bay.

Enteromorpha salina Kuetzing (Figs. 11, 12, 49–51)

Mature fronds to 15 cm tall, tubular, and slender, seldom exceeding 0.5 cm in diameter; branches erect and thorn-like, sometimes opposite, of two or more rows of cells, or in the youngest parts, of a single series; cells thickwalled and square in surface view; in younger parts 8–10 × 12 μ, becoming quadrangular or rectangular, 10–12 × 18–22 μ, in longitudinal series throughout; pyrenoids 2–3.

Enteromorpha salina is restricted to warmer waters from North Carolina south along the Atlantic coast and into the Gulf of Mexico. This species was collected once on the southwest jetty at Pt. Aransas during March. No generalizations concerning typical habitat or seasonal periodicity can be made from this chance encounter.

Enteromorpha flexuosa (Wulfen) J. G. Agardh (Figs. 13, 14, 52–54)

Plants 1–2 dm tall and 0.5–1.5 cm wide, usually simple or occasionally divided at the base into 2–3 similar branches which taper to a filiform stipe below; fronds initially flattened, becoming cylindrical and intestiniform above; cells thickwalled, polygonal to subrectangular, 10–12 × 15–18 μ, in longitudinal rows below and irregularly disposed above; plastid parietal, forming a hollow cylinder in older cells; pyrenoids 2–3.

This species is typical of warmer waters and is confused with *E. intestinalis* in such localities; *E. flexuosa* differs from this species in that its cells are subrectangular rather than round and are in light series except in the older parts.

Enteromorpha flexuosa is found in calm waters just below low tide level in most of the tropics and warm-temperate waters from North Carolina, throughout the Gulf of Mexico, to Uruguay. In this study, it was found in sheltered locations in Aransas Bay and at Pt. Aransas. It was most abundant during late winter and disappeared during the summer.

Enteromorpha prolifera (Muell.) J. G. Agardh (Figs. 15, 16, 57–59)

Fronds 20–30 cm long and 1.5 to 5 mm in diameter, tubular, and proliferously branched; branches similar to the main axis, often 5 cm long and arising along its entire length; cells typically quadrangular to subrectangular, 10–12 × 18–20 μ, in younger parts in longitudinal series but becoming less orderly in older parts; pyrenoids 1–2.

This species is somewhat similar to *Enteromorpha compressa* and *E. intestinalis* in northern waters but is distinguished in the study area by its distinct main axis which bears proliferous branches along its entire length.

Enteromorpha prolifera occurs in sheltered bays where it grows at low tide level. It has been reported along most of the Atlantic coast of North America from James Bay to Florida, from the Gulf of Mexico, and from tropical South America. It was found in sheltered locations in Aransas Bay and at Pt. Aransas during the winter and early spring.

3. Analysis of Collected Material

Determination of the *Ulva* and *Enteromorpha* species occurring on the Texas coast are often difficult despite the detailed descriptions given above. The dichotomous key for *Enteromorpha* relies largely on macroscopic morphological characters although many authors (Bliding 1955, 1960, 1963; Dangeard 1958, 1959, van den Hoek 1964) maintain that criteria such as frond size and color, and degree and pattern of branching are too variable to be reliable. According to Dangeard (1951, 1959), Føyn (1955, 1958) and Bliding (1968), variability among *Ulva* species creates similar taxonomic problems.

These same authors (Bliding 1938; Dangeard 1958; Føyn 1958) have presented a list of characters which are reportedly more stable. They include the nature of the reproductive bodies, interfertility of species with sexual swarmers, zygote development, pyrenoid number, and cell size and shape.

Van den Hoek (1964) considered mode of reproduction and interbreeding behavior to be the most constant criteria. Unfortunately, information concerning most of these characters, especially those generally agreed to be of primary importance, is unavailable unless cultural studies are undertaken. Morphological characters such as cell size and shape and pyrenoid number which can be used for the identification of collected material often overlap for several species.

An analysis of herbarium material prepared during this investigation was undertaken in an attempt to find a means of identifying species with some certainty without resorting to cultural studies. Similar work has been most useful in clarifying taxonomic problems in other groups of algae. Russell (1966) reduced the complex of attached forms of *Ectocarpus* in Britain to two species. A graphic presentation of his measurements of vegetative filaments and plurilocular sporangia demonstrated the existence of two fairly descernible groups which have a few overlapping characters. Stewart's (1968) investigation of *Pterocladia pyramidale* and South and Burrow's (1967) work with *Chorda filum* were likewise successful in using an analysis of herbarium material to clarify the taxonomy of these genera.

Bergquist (1959) used discriminatory analysis, a statistical method of measuring and plotting several variables simultaneously, to demonstrate that the various ecological forms of *Hormosira banksii* in New Zealand belong to one species.

An analysis was made of frond length and width, and of cell width and length for all eight species encountered in this study. The range and mean were determined for each character and plotted on a linear graph (Figs. 17–20). Measurements were made on 25 plants of each species, except *Enteromorpha prolifera* and *E. salina*. Collected material was limited for these two species, which were represented by 15 and eight specimens, respectively. Cellular dimensions were recorded from material in surface view, except for *Ulva* species in which the blades were viewed in transverse section.

In general, the results confirm the findings of Bliding (1963, 1968) and others that morphological characters are variable within the Ulvaceae. However, several generalizations can be made. *Enteromorpha flexuosa* (Fig. 17) has the longest fronds and the greatest variability of frond length of all the *Enteromorpha* species at Pt. Aransas; *E. flexuosa* fronds are also the broadest and have the greatest variability in frond width (Fig. 18). *Enteromorpha lingulata* has the shortest frond length (Fig. 17) but has a frond width similar to the other species. *Enteromorpha prolifera* fronds (Fig. 17) are usually longer than those of other species. *Enteromorpha prolifera* fronds (Fig. 17) are usually longer than those of the other species, but they never reach the extreme proportions encountered with the fronds of *E. flexuosa*. *Enteromorpha salina* (Fig. 17) has the shortest range of frond length, but the specific measurements are not distinct from those of either *E. clathrata* or *E. ramulosa*. *Enteromorpha clathrata* and *E. ramulosa* have similar frond lengths (Fig. 17), but the fronds of *E. ramulosa* tend to be broader (Fig. 18). Cell width measurements are strikingly similar for all the *Enteromorpha* species (Fig. 19). Cell length measurements are slightly more diverse, *E. flexuosa* having the shortest cells and *E. lingulata* the longest (Fig. 20).

An analysis of the above characters demonstrated a fairly clear distinction between the two local *Ulva* species, *U. lactuca* and *U. fasciata* (Figs. 17, 18). *Ulva lactuca* is generally much shorter than *U. fasciata*, which is often three to four times longer than the former (Fig. 17). *Ulva lactuca* has a much broader frond, which is never linear as is that of *U. fasciata* (Fig. 18). In transverse sections of blades of *U. lactuca* the cells appear nearly square, being almost as broad as tall (Fig. 44), while in sections of *U. fasciata* the cells are distinctly rectangular, and are often twice as tall as broad (Fig. 43).

Although this analysis of individual characters allows for generalized specific distinctions, it shows that no one character can adequately circumscribe the species of Ulvaceae. Following the work of Bergquist (1959), an attempt was made to compare simultaneously two different criteria of morphologically similar species. The results of plotting two variables simultaneously are presented in Figs. 21–24. Measurements were made on 25 plants of each species, except for *Enteromorpha prolifera*, which was represented by eight specimens, and *Ulva fasciata* and both varieties of *U. lactuca*. which were represented by 15 specimens each.

A simultaneous comparison of frond length and width in Figure 21 shows that

Ulva lactuca and *U. fasciata* are distinct. *Ulva fasciata* fronds are linear, while those of *U. lactuca* are never as narrow and tend to be as broad as tall. The two varieties of *U. lactuca*, *U. lactuca* v. *rigida* and *U. lactuca* v. *latissima* are indistinguishable on this basis but can be separated if a more detailed set of criteria is used.

Enteromorpha ramulosa and *E. clathrata* represent a cline when maximum cell length and minimum cell width are compared (Fig. 22). Although these two species have distinct cell shapes in surface view and can be distinguished on this basis, cell measurements alone seem to be of no value for species circumscription.

Enteromorpha prolifera and *E. flexuosa* can be separated when maximum cell length and minimum cell width are compared (Fig. 23). Unlike *E. ramulosa* and *E. clathrata* which differ in cell shape, *E. prolifera* and *E. flexuosa* cells are similar in shape but differ in that cells of the former have a greater length to width ratio than those of the latter.

On the basis of cellular dimensions, *Enteromorpha flexuosa* is even more distinct from *E. lingulata* than from *E. prolifera*. *Enteromorpha lingulata* cells have a greater length-to-width ratio than those of *E. flexuosa*. This criterion coupled with the distinctness of cell shape for the two species can be used to make identifications more certain (Fig. 24).

In conclusion, simultaneous analysis of two separate characters provides additional information for more accurate interspecific distinctions for some of the Ulvaceae. However, this method of interpreting herbarium data should be used cautiously since morphological characters, even when considered in pairs, are so flexible as to provide only a general idea of the taxonomic delimitation of a species.

B. Cultural Studies

1. Cultural Conditions

Results of the preceding analysis of collected material indicated that additional information was required to delimit successfully the species of Ulvaceae occurring in Port Aransas area. Van den Hoek (1964), in his review of contemporary algal taxonomy, suggested that the most constant criteria for individual species include aspects of their life history which are available only by observing material in culture. Van den Hoek (1963) successfully utilized cultural studies in his investigation of some European species of *Ulva*. Chihara investigated the life histories of several Chlorophycean genera in culture including *Collinsiella* (1958), *Capsosiphon* (1967a), and *Collinsiellopsis* (1967b). Dangeard (1961b) used culture techniques to study *Blidingia*. Work on *Monostroma* by Yamada and Kanda (1941), Kornmann (1962, 1963), Gayral (1964b, 1965), Yamada and Tatewaki (1965) and Dube (1967) have shown that a knowledge of the life history is an essential prerequisite to constructing a practical system of classification for this genus.

Many workers have utilized the information obtained from cultural studies of the Ulvaceae to supplement taxonomic characters available from the analysis of herbarium specimens. Bliding (1938) was the first to use this approach with *Enteromorpha*, and he succeeded in delimiting many of the European species in

his subsequent papers (Bliding 1939, 1944, 1948a,b, 1955, 1963). Yamada and Saito (1938) and Arasaki and Shihira (1959) have cultured many Japanese species of *Enteromorpha*. A number of French phycologists have followed the methods of Dangeard (1957, 1958, 1959, 1961a,b), who relied largely on cultural techniques. They include Comps, (1961), Gayral (1960, 1961), Parriaud (1961, 1964) and Villot (1963). Several investigators conducted cultural investigations on species of *Ulva* (Dangeard 1951, 1961a, Cauro 1958; Gayarl 1964a; Bliding 1968; Chihara 1968, 1969). Føyn (1955, 1958, 1959) has presented a series of comprehensive studies on the European species of *Ulva*.

This widespread success from incorporating information on life histories into a more comprehensive list of taxonomic criteria for the Ulvaceae and closely related Chlorophycophyta encouraged a similar cultural study of the Ulvaceae of the Port Aransas area. Initially, it was necessary to determine a combination of environmental factors which would promote rapid growth of plants with normal morphology in culture. Algae were cultured in six different media including defined synthetic seawater and seawater enrichments as described under Materials and Methods. Von Stosch's seawater enrichment as cited by Ott (1966) was finally utilized because it promoted the best growth and was easily prepared. An attempt was made to find a satisfactory combination of light intensity, photoperiod, and temperature. Eight different environmental combinations were available to the author (Table 2), and these were employed to obtain a preliminary indication of which factors would be most conducive to growth of the organisms in culture.

Germlings of *Enteromorpha clathrata* were introduced into four types of containers: 15-ml and 50-ml Petri dishes. 50-ml Erlenmeyer flasks, and 250-ml covered beakers. Two containers of each size were placed in each incubator. Von Stosch's enrichment medium as cited by Ott (1966) was used in this and all subsequent experiments. The plants remained under the conditions outlined in Table 2 for six weeks. After that time several criteria, including plant size and color and normalcy of cellular appearance, were employed to determine the most satisfactory environment for growth. According to this subjective evaluation, growth was best in culture chambers seven and eight (light at 200 ± 20 ft-c on a 12-hr light, 12-hr dark cycle, and temperatures 20 or 25 C) and in the 250-ml

TABLE 2

Culture regimes prevailing in eight incubators

Cultural Chamber Number	Light Intensity in ft-c	Temperature in C	Photoperiod Light : Dark
1	50 ± 10	23 ± 2	14:10
2	150 ± 20	23 ± 2	14:10
3	250 ± 20	23 ± 2	14:10
4	300 ± 20	23 ± 2	14:10
5	50 ± 10	23 ± 2	14:10
6	100 ± 10	12 ± 2	8:16
7	200 ± 20	23 ± 2	12:12
8	200 ± 20	18 ± 2	12:12

beakers. Although growth was best in the largest containers, they were not used again in this study because their size would have entailed the use of prodigious quantities of media and space. Growth in the 50-ml containers was normal, although slower. Thus, 50-ml Erlenmeyer flasks were used during the study because of their convenient size and ease of handling.

Subsequently, another set of environmental combinations became available and was utilized to gain more information on optimum conditions for algal growth. Five incubators were programmed with a photoperiod of 14 hr light and 10 hr dark, and a light intensity of 200 ± 20 ft-c; temperatures were different in each incubator, being 9 ± 1, 13 ± 2, 18 ± 2, 22 ± 2, and 28 ± 2 C. Erlenmeyer flasks with 40-ml of media were inoculated with germlings of four species: *Ulva fasciata, Enteromorpha clathrata, E. ramulosa,* and *E. lingulata.* Two flasks of each species were placed in the incubators. The plants were incubated for six weeks. A subjective evaluation of growth was made. All four species had a wide latitude of temperature tolerance (Figs. 101–104). Although frond size was often similar under all of these conditions, cells usually appeared to be more nearly normal in shape and arrangement at temperatures of 18 and 22 C. On the basis of these two preliminary experiments, the following cultural conditions were employed for the life history studies: a 200 ft-c light intensity, a temperature of 22 C, and a 12 hr daylength.

2. Life History Studies

The following eight species of Ulvaceae from Port Aransas, Texas, were cultured to determine their life histories: *Ulva lactuca, U. fasciata, Enteromorpha clathrata, E. salina, E. ramulosa, E. lingulata, E. prolifera,* and *E. flexuosa.* The life histories of seven of these species could be separated into two distinct types. *Ulva lactuca, U. fasciata, E. clathrata, E. lingulata,* and *E. salina,* included in the first type, have an alternation of isomorphic gametophytic and sporophytic generations as outlined by Bliding (1963, 1968). Biflagellate gametes tended to be slightly unequal, the females rounder and larger than the smaller, thinner males. Both male and female gametes were capable of parthenogenetic development into male and female gametophytes, respectively. Copulation occurred when compatible gametes of opposite mating strains were mixed. Not all male and female gametes were compatible. However, when gametophytes were located which produced compatible gametes, they could be parthenogenetically reproduced and used as a constant and reliable source of compatible gametes. Zoospores were always quadriflagellate, noticeably larger than gametes, and positively phototactic when intially released but becoming negatively phototactic after a few hours of motility. No reproductive variations were observed; the zoospores always germinated into male and female gametophytes in the approximate ratio of 1:1. Zoospores were produced only by sporophytes resulting from the successful copulation of two gametes of opposite sexes. Zygotes typically germinated within two days.

The second type of life history was observed in *Enteromorpha flexuosa* and *E. ramulosa.* Both of these species lack an alternation of gametophytic and sporophytic generations. They reproduced by positively phototactic quadriflagellate

zoospores. No biflagellate zoospores were ever observed in cultures of *E. flexuosa* but they were occasionally noted for *E. ramulosa*. Copulation of swarmers was never observed. Evidently the isolates of these species lack a means of sexual reproduction.

Enteromorpha prolifera could not be grouped with either of the above types. This species includes a race which reproduces with an alternation of gametophytic and sporophytic generations, as well as races which reproduce solely by bi- and quadriflagellate swarmers. In some cultures considerable variability occurred in the sequence of bi- and quadriflagellate zoospore production.

A more detailed analysis of the results for each species gave information concerning the morphology and behavior of the reproductive bodies, the length of time necessary to complete a reproductive cycle, and the type of life history involved. These data are summarized below for the taxa investigated.

a. Reproductive Histories

Ulva lactuca

A mature sporophyte was collected from an intertidal bay beach one mile south of Rockport on April 18, 1968. The frond released zoospores which germinated into gametophytes. These plants became sexually mature within six weeks. Zoospores were quadriflagellate and $5 \times 9\ \mu$. Gametes were biflagellate and positively phototactic; males $3 \times 7\ \mu$, females 4×7–$8\ \mu$. Both male and female gametes were able to develop parthenogenetically. Three complete generations were observed during a 12-month period.[2] There was no evidence of any irregularity in this life history. These results are in agreement with the findings of Gayral and Mazancourt (1958) and Bliding (1968), who reported a normal alternation of generations for this species in Europe.

Ulva fasciata

Two isolates were maintained for this species. One originated from zygotes formed by the fusion of gametes of opposite mating types which were simultaneously liberated from unisexual gametophytes collected from the Pt. Aransas southwest jetty on August 25, 1968. The second culture originated from zoospores released from a sporophyte collected on the Pt. Aransas southwest jetty on October 21, 1968. Three complete generations have been observed for the first culture over an 8-month period, and two complete generations observed for the second culture over a 6-month period.

Quadriflagellate zoospores were $5 \times 9\ \mu$ (Fig. 92) and completely identical to those of *Ulva lactuca*. The gametes of *U. fasciata* were slightly smaller than those of *U. lactuca*; males were $3 \times 5\ \mu$, and females $4 \times 7\ \mu$ (Fig. 91). Both male and

[2] In races reproducing by an alternation between gametophytic and sporophytic phases, the words "complete generation" signify the development of gametophytes from zoospores, the subsequent mating of compatible gametes, zygote formation, the development of the zygotes into sporophytes, and the production of zoospores from the latter. In races reproducing by asexual zoospores only, a complete generation is meant to include the development of plants from zoospores and the subsequent production of zoospores by these plants.

female gametes were able to develop parthenogenetically but not as readily as those of *U. lactuca*. Compatible gametes clumped and paired before copulation occurred (Fig. 91). Quadriflagellate zygotes (Fig. 93) were motile for a few minutes and negatively phototactic. Germination began within two days. The germlings differentiated into holdfast and blade cells after the first cellular division. Young germlings were initially uniseriate but became hollow and then flattened (Fig. 94). The fronds became sexually mature within eight weeks.

These results are in agreement with the findings of Cauro (1958) for this species on the coast of Morocco. However, Gayral (1964a) found races which lacked a sexual phase and reproduced by an alternation of bi- and quadriflagellate zoospores.

Enteromorpha clathrata

A mature sporophyte was collected from the Rockport breakwater on December 18, 1967. The frond released zoospores which germinated into gametophytes. These plants produced gametes within three weeks. Zoospores were quadriflagellate and 6×8–$9\ \mu$. Gametes were biflagellate (Figs. 87–90) and positively phototactic, males $3 \times 5\ \mu$, and females $4 \times 7\ \mu$. Both male and female gametes readily developed parthenogenetically. Compatible gametes clumped and paired before copulation occurred (Figs. 87–90). The quadriflagellate zygotes were motile for a few minutes and negatively phototactic. Germination began within two days (Fig. 90). Young germlings were initially uniseriate but soon became tubular. Six complete generations were observed during 16 months.

These results agree with those of Dangeard (1958) and Bliding (1963), who found a regular alternation of isomorphic gametophytic and sporophytic generations in *Enteromorpha clathrata*.

Entermorpha lingulata

A mature sporophyte was collected from the Pt. Aransas southwest jetty on October 21, 1968. The frond released zoospores which germinated into gametophytes. These plants produced gametes within three weeks. The zoospores were quadriflagellate and 5–6×8–$9\ \mu$, and the gametes biflagellate, males $3 \times 5\ \mu$ and females $5 \times 7\ \mu$. Both male and female gametes developed parthenogenetically. Compatible gametes clumped and paired before copulating. The quadriflagellate zygotes were motile for a few minutes and negatively phototactic. Young germlings were initially uniseriate but soon became tubular and branched from the base. Three complete generations were followed during five months.

No published information could be found for the life history of this tropical species which apparently has a typical alternation of isomorphic gametophytic and sporophytic generations.

Enteromorpha salina

A mature sporophyte was collected from a tidal pool on the Pt. Aransas southwest jetty on March 23, 1968. The frond released zoospores which germinated into gametophytes. These plants produced gametes within three weeks. The zoo-

spores were quadriflagellate and 6 × 8–10 μ, while the gametes were biflagellate, the males 3 × 5 μ, and the females 4 × 7 μ. Both male and female gametes developed parthenogenetically. Compatible gametes clumped and paired before copulating. The quadriflagellate zygotes were motile for a few minutes and negatively phototactic. Young germlings were initially uniseriate but soon became tubular. Five complete generations were observed during 12 months.

No published information could be found for the life history of this tropical species, but it appears to have a regular alternation of isomorphic gametophytic and sporophytic generations.

Enteromorpha flexuosa

Two completely identical races were maintained for this species. Both originated from zoospores released from different sporophytes.[3] One was collected from an intertidal bay beach one mile south of Rockport on February 29, 1968, and the other was collected from a tidal pool on the Pt. Aransas jetty on March 23, 1968. Six complete generations have been observed for the first culture in 14 months, and three complete generations noted for the second culture in 12 months.

The zoospores were quadriflagellate and positively phototactic. Zoospores in the first culture were 6–7 × 10–11 μ (Fig. 79) and slightly smaller in the second culture, nor was copulation of zoospores observed. Germination of the zoospores began within a few days after they settled. Young germlings were initially uniseriate but soon became tubular. Dangeard (1958) reported a similar asexual cycle for *E. flexuosa* in which reproduction was by means of quadriflagellate zoospores. Bliding (1963) reported races of the same species which reproduced solely by zoospores as well as types which could produce bi- and quadriflagellate zoospores, simultaneously or separately, and races with a perfectly normal alternation of isomorphic gametophytic and sporophytic generations. Evidently this species includes several reproductively distinct types. It is not known whether these other forms occur on the Texas coast or are merely uncommon and were overlooked in this study.

Enteromorpha ramulosa

A mature sporophyte was collected from an intertidal bay beach one mile south of Rockport on January 21, 1969. The zoospores were quadriflagellate and 6 × 10 μ. Five generations have been observed in four months. The first three generations involved quadriflagellate zoospores only and were thus completely similar to the life history outlined for *Enteromorpha flexuosa*. However, some fourth-generation plants simultaneously produced both bi- and quadriflagellate swarmers, 3 × 5 μ, and 6 × 9 μ, respectively (Figs. 95, 96). Both types of swarmers

[3] Since the nuclear condition of these plants was not known to be diploid, they were not necessarily *bona fide* sporophytes (Ramanathan 1936; Føyn 1934). However, plants producing quadriflagellate swarmers or even asexual biflagellate swarmers were referred to as sporophytes in this study in accordance with the use of the term by others (Dangeard 1961a; Bliding 1963, 1968; Gayral 1967).

were apparently zoospores as they settled without any evidence of copulation and germinated into plants producing only quadriflagellate zoospores.

The significance of this temporary "abnormality" is not understood. It may have been a response to undetermined and unfavorable environmental factors, or merely an alternate form of reproductive swarmers as reported by Bliding (1963) for *Enteromorpha flexuosa*. Since Hartman (1929), Dangeard (1958) and Bliding (1963) have reported an alternation of isomorphic gametophytic and sporophytic generations for *E. ramulosa*, the appearance of these biflagellate swarmers may represent a vestigal, nonfunctional sexual phase. It is not known whether races with a typical sexual cycle are also present on the Texas coast.

Enteromorpha prolifera

This species could not be grouped with either of the life-history types discussed above. Four different isolates were maintained and all four had distinct life histories.

Isolate 1 originated from a sporophyte collected from an intertidal bay beach one mile south of Rockport on February 25, 1968. The frond released zoospores (Fig. 82), which were quadriflagellate and 6–8 × 10–11 μ, and which germinated into gametophytes. These plants produced gametes within four weeks (Figs. 80, 81). Compatible gametes clumped and paired before copulating (Fig. 83, 84). The quadriflagellate zygotes (Figs. 85, 86) were motile for a few minutes and negatively phototactic. Four complete generations were observed during 12 months. This race apparently has an alternation of gametophytic and sporophytic generations.

Isolate 2 originated from a sporophyte collected at the same time and place as culture 1. Its zoospores were quadriflagellate and 6 × 8–9 μ; the gametes were biflagellate; males 3 × 5–6 μ, females 4 × 7 μ. Both male and female gametes developed parthenogenetically. Other particulars of the life history were identical to those of culture 1 through the third generation. At that time certain female gametophytes produced positively phototactic quadriflagellate swarmers, 5–6 × 8–10 μ. These swarmers developed parthenogenetically into gametophytes producing female gametes as described above. During the fifth generation, certain male gametophytes produced positively phototactic quadriflagellate swarmers completely similar to the other atypically derived zoospores. These swarmers developed parthenogenetically into gametophytes producing male gametes. The significance of this temporary "abnormality" is not understood. If it were a response to unfavorable conditions of culture, it is difficult to explain why zoospore formation occurred at different times in male and female cultures. Føyn (1934, 1958) and Kornmann (1956) have reported instances of polyploidy occurring in the Ulvaceae. They imply that plants which develop parthenogenetically from gametes can become diploid and thus produce quadriflagellate zoospores. No satisfactory cytological evidence has been offered in support of this phenomenon in the Ulvaceae. Since the occurrence of these atypical swarmers, two completely normal reproductive cycles have been observed.

Isolate 3 originated from a sporophyte collected from the Pt. Aransas southwest

jetty on February 26, 1968. The frond released zoospores which germinated into plants producing biflagellate swarmers at maturity. The zoospores were positively phototactic and 6 × 8–9 μ, the biflagellate swarmers were 4 × 7 μ. No copulation for either type of motile cell was ever observed. This alternation between plants producing biflagellate swarmers and plants producing quadriflagellate zoospores has continued through six generations in 12 months. This race apparently has no sexual phase. Gayral (1964a) obtained a mutant of *Ulva fasciata* in culture which lacked a sexual phase and reproduced similarly by an alternation between sporophytic generations sequentially producing bi- and quadriflagellate zoospores.

Isolate 4 originated from a frond collected at the same time and place as the frond taken for culture 3. The frond initially released biflagellate swarmers, 3–4 × 5–7 μ. Attempts to mate these swarmers with gametes of both sexes from cultures 1 and 2 were unsuccessful. It is not known whether this race is reproduced by biflagellate zoospores or by nonfunctional gametes. Three parthenogenetic generations as outlined above were observed. Fronds of the fourth generation were found to produce quadriflagellate zoospores. It is not known whether this development represents a chromosome doubling as reported by Føyn (1934) or a mutation as reported by Gayral (1964a).

Bliding (1963) reported considerable variability in the life history of *Enteromorpha prolifera.* He found races with a completely typical alternation of isomorphic generations as reported in this study for culture 1. He also found races which reproduced by bi- or quadriflagellate zoospores, but none that demonstrated a serial alternation as in cultures 3 and 4. It would be interesting to know if these sequential alternations are unique to *Enteromorpha prolifera* on the Texas coast or are more general in occurrence, but unreported, due to lack of continuous observation of material in culture.

In summary, seven of the eight species of the Ulvaceae investigated by the writer had a life history characterized either by an alternation of gametophytic and sporophytic generations, or by a loss of the sexual phase and reproduction solely by asexual zoospores. One species, *Enteromorpha prolifera,* had several types of life histories including an alternation of sexual and asexual generations, and several variations involving the sequential production of bi- and quadriflagellate zoospores. Similar variations for a single species have been reported in *Enteromorpha linza* (Bliding 1939; Niizeki 1957, cited by Bliding 1963; Dangeard 1958; Arasaki and Shihira 1959), *Enteromorpha prolifera* (Bliding 1963), *Enteromorpha flexuosa* (Dangeard 1958, Bliding 1963) and in *Ulva fasciata* (Cauro 1958; Gayral 1964a). Furthermore, the variations found in these widely studied species may be an indication that other species have undetected alternate forms of reproduction. Therefore, data from life-history studies should be applied cautiously to taxonomic problems.

The results of this investigation indicate that life-history studies should be applied cautiously to taxonomic problems.

The results of this investigation indicate that life-history data can be of value, in some instances, in delimiting the species of Ulvaceae found on the Texas coast. *Enteromorpha clathrata* and *E. ramulosa* are both profusely branched and can be confused. However, their life histories are dissimilar: *E. clathrata* reproduces

with an alternation of generations and *E. ramulosa* reproduces by asexual swarmers only. Therefore, these species can be readily separated by culturing doubtful material and observing the nature of the reproductive bodies. Similarly, branched material of *Enteromorpha flexuosa* can resemble *E. prolifera.* Once again critical observation of material in culture will provide information to delimit these two species, as *E. flexuosa* reproduces with quadriflagellate zoospores only, while *E. prolifera* reproduction includes biflagellate swarmers which act either as gametes or an alternate form of zoospore.

Enteromorpha salina and *E. lingulata* are morphologically distinct species and do not require culturing for correct identification. *Ulva lactuca* and *U. fasciata* are also distinct and can be identified on the basis of morphological characters. Since all of these species have an alternation of sexual and asexual generations, they cannot be identified by their life histories.

It is generally agreed that members of the Ulvaceae have an alternation of generations with isomorphic or nearly isomorphic individuals (Bliding 1963, 1968; Gayral 1967). However, Scagel (1960) has described a race of *Enteromorpha intestinalis* which arose from an isolate of *Collinsiella.* The *Enteromorpha* material reproduced itself with quadriflagellate zoospores but failed to give rise to *Collinsiella.* More detailed cultural studies on *Collinsiella* by Chihara (1958, 1959, 1960) failed to confirm the presence of an alternation of heteromorphic phases. Although closely related taxa such as *Monostroma grevillei* (Kornmann 1962) and *Ulvopsia* (Gayral 1967) are known to have an alternation of heteromorphic gametophytic and sporophytic generations, the results of this investigation and studies by other workers indicate that heteromorphic phases probably do not occur in the life histories of the Ulvaceae.

b. Germling Development

Germlings from zoospores, zygotes, and parthenogenetic gametes differentiated into a frond cell and a rhizoidal cell after the first cellular division. All cells which originated from the rhizoidal cell contributed to the basal attachment system while cells which developed from the frond or blade cell contributed to the erect, photosynthetic portion of the plant. After this initial differentiating division, germling development proceeded according to one of two distinct sequences. In *Ulva lactuca, U. fasciata, Enteromorpha clathrata, E. ramulosa,* and *E. lingulata,* the basal cell did not proliferate until the blade portion had undergone numerous divisions. Thus, the germlings consisted of a single attaching cell and a uniseriate filament (Figs. 97, 98). In *Enteromorpha flexuoso, E. prolifera,* and *E. salina,* the basal cell proliferated into a multicellular rhizoidal system before the frond cell completed its first division (Figs. 99, 100). By the time the uniseriate filament developed into a tubular frond, these distinctions had disappeared. In individuals of the first type, rhizoidal development preceeded rapidly after the initial dormancy. In the second type, rhizoidal developments did not continue until a tubular frond was formed. Thus, ten-day-old germlings of all species were nearly identical. Only the primary stages were distinct because of the temporary differential growth of the basal and erect portions of the plants.

There seems to be a general relationship between germling development and life-history type. Except for *Enteromorpha ramulosa*, all species with an initial blade development reproduced by an alternation of gametophytic and sporophytic generations. Except for *E. salina*, all species with an initial rhizoidal development reproduced by asexual swarmers only. It might seem that sporophytes tend to have a developmental sequence distinct from gametophytes. However, both gametophytic and sporophytic germlings of *Ulva lactuca*, *U. fasciata*, *Enteromorpha clathrata*, and *E. lingulata* are identical. Therefore, the type of germling development is more nearly characteristic of the species than of either the gametophytic or sporophytic phase of the life history.

Gayral (1967) reported a similar species-related developmental sequence for germlings of Ulvaceae. *Ulva lactuca*, *U. fasciata*, *Enteromorpha compressa*, and *E. linza* germlings have an initial frond development, according to Gayral, while *E. tubulosa* and *E. sancti joannis* have an initial rhizoidal development.

c. Frond Morphology

Many authors have reported that the extreme variability of morphological characters within the Ulvaceae often makes specific determinations impossible. Klugh (1922) found extensive ecological polymorphism in *Enteromorpha clathrata*. He collected specimens of this species which were so atypical that an identification could not have been made had he not observed so many specimens that a morphological gradient became apparent between normal and atypical forms. Dangeard (1957) reported that *Enteromorpha prolifera*, *E. compressa*, and *E. intestinalis* could be quite similar due to secondary proliferations. Arasaki and Shihara (1959) found that the morphology of *Enteromorpha linza* in nature can be altered by environmental factors. Taylor (1957, 1960) warned that specific identifications for *Enteromorpha* are sometimes impossible because of morphological variations.

Consequently, the eight local species of Ulvaceae were cultured under uniform conditions in an attempt to eliminate phenotypic variations which are apparently responsible for many atypical growth forms. A detailed analysis of the results of this cultural study has provided additional information as a basis for separation of species.

Ulva lactuca

Cultured material of this species was noticeably different from specimens collected in nature. The fronds were considerably smaller, measuring 1 × 4 cm, and never attained the massive proportions of collected material (Figs. 25, 26). Also, there was a tendency for the distromatic blade to separate near the base and thus to form an intestiniform stalk. Despite these differences, frond thickness and cellular characters were remarkably similar for plants in culture and collected material (Fig. 65). Transverse sections of the frond and surface examination revealed that characters such as cell shape, dimensions, and arrangement were constant and that they agreed with the descriptions given above for collected material (Fig. 65).

There was no evidence of sexual dimorphism in the cultured material. Gametophytes of both sexes and sporophytes were all similar. However, Smith (1947) reported that gametophytes and sporophytes of Pacific coast species of *Ulva* in nature could be distinguished on the basis of their distinct reproductive periodicities.

Gayral (1967) reported similar results in *Ulva lactuca*. Although cellular characters were constant enough to allow identifications to be made, the fronds were often stunted and basally tubular.

Ulva fasciata

Cultured material of this species was completely similar to specimens collected in nature. The fronds were narrow and linear, 1–2 cm wide × 15 cm long. They probably could have attained even greater lengths if larger culture containers had been utilized. Sexual dimorphism was apparent in the cultured material (Figs. 27, 28). Male gametophytes and sporophytes were noticeably larger than female gametophytes. This phenomenon was not confirmed in collected material of this species.

Cellular characters of gametophytes of both sexes and of sporophytes in cultured and collected material were similar. The cells were polyhedral and rounded, irregularly arranged (Figs. 63, 64), and in agreement with the dimensions cited for collected material.

Enteromorpha clathrata

Cultured material of this species was similar to specimens collected in nature. The fronds were long and delicately branched but did not attain the degree of branching typical of plants in nature. Gametophytes of both sexes and sporophytes were all morphologically identical (Fig. 37).

Cellular characters for cultured material were in agreement with those cited for collected material, except that the cells tended to be shorter, with a maximum length in surface view of 20 μ instead of 24 μ or more.

Enteromorpha lingulata

Material of this species grew poorly in culture. Although the fronds were morphologically similar to collected material, they appeared stunted and seldom acquired more than two or three basal branches. Sexual dimorphism was noted in the cultures (Figs. 39, 40). The males were 5–8 cm tall and more than twice as large as females and sporophytes which seldom exceeded 2–3 cm in length. While these plants differed in frond size, their cellular characters were constant for all three life forms and in agreement with data from herbarium specimens (Figs. 75, 76).

Enteromorpha salina

Cultured plants of this species demonstrated the most striking sexual dimorphism observed in this study (Figs. 29–31). Male gametophytes were 12–15 cm

tall and much larger than females which seldom exceeded a length of 3 cm. Sporophytes were about the same size as males (Fig. 30). Cellular characters were constant and closely agreed with data from herbarium material (Figs. 66–68).

Enteromorpha flexuosa

Plants of this species grew well in culture but tended to be shorter and thinner than plants in nature. This phenomenon was noted by Gayral (1967) for cultures of *Enteromorpha linza,* a species which has similar intestiniform and inflated fronds. Fronds of *Enteromorpha flexuosa* in culture was 8–10 cm long and unbranched (Fig. 38). However, basal proliferations often formed a cushion of short interwoven filaments.

Cellular characters for cultured material were in agreement with the descriptions cited for collected material except that cells tended to be longer, reaching a maximum length of 22 μ, instead of 18 μ (Figs. 77, 78).

Enteromorpha ramulosa

Plants of this species tended to sporulate prematurely in culture, so that they seldom achieved an appreciable size, and rarely exceeded a length of 5 cm (Fig. 32). Cellular characters were generally similar for cultured and collected material (Figs. 69, 70), except that plants in culture had 2–4 pyrenoids per cell instead of the 4–7 pyrenoids common in collected specimens.

Enteromorpha prolifera

Plants of this species grew well in culture and exhibited a typical morphology. Plants from races with different life histories were generally indistinguishable. However, male plants were noticeably more branched than females (Figs. 33, 34). This was true for both races having an alternation of sexual and asexual generations. Plants from races with reproduction by asexual swarmers were less branched than either male or female gametophytes (Figs. 35, 36). Cellular characters were remarkably constant for plants from all four races and in close agreement with data from collected material (Figs. 71–74), except that plants in culture had 2–3 pyrenoids instead of the 1–2 common in collected material.

In summary, these cultural studies provided information which can be of use in selecting an appropriate species for subsequent investigations of more specialized scope. These results suggest that *Ulva lactuca* is not sufficiently suited to cultural studies to warrant its extensive use. *Ulva fasciata* should be given preference since it grows more rapidly and normally than *Ulva lactuca* and because it is sexually dimorphic and thus lends itself to genetic experiments similar to those conducted by Føyn (1955, 1958).

Certain *Enteromorpha* species grew more easily than others and thus are more suitable for studies of gross morphology in culture *Enteromorpha clathrata, E. salina, E. flexuosa* and *E. prolifera* developed large, normal fronds, while those of *E. lingulata* and *E. ramulosa* were usually stunted.

Enteromorpha salina, E. lingulata, and races of *E. prolifera* demonstrated sexual dimorphism and thus lend themselves to investigations of sex-linked inheritance. It is interesting to note that in all instances of sexual dimorphism, the male gametophytes were considerably larger or more heavily branched than the female. Sex determinations were based on size and shape of gametes and color of fertile areas in reproductive fronds. These same characters have been used by all investigators and, thus, are considered to be reliable criteria for sex determination. Such extensive sexual dimorphism has not been previously reported except for races of *Enteromorpha linza,* by Arasaki and Shihara (1959). They reported that male and female gametophytes from nature were sometimes distinct from each other and from sporophytes.

Cultural studies provided data to confirm the reliability of certain taxonomic criteria. Although many authors, including Klugh (1922), Dangeard (1957), Taylor (1957, 1960), Bliding (1963) and Gayral (1967), discouraged the use of branching for species determinations, this character was found to be reasonably constant and could be used in conjunction with other taxonomic characters. However, frond branching should not be relied upon as a primary, and definitely not as an exclusive, taxonomic character when other information is available.

Van den Hoek (1963) found that cell shape and arrangement and plastid shape are among the most constant characters in culture and demonstrate the best agreement with collected material. Pyrenoid number and cellular dimensions are similarly considered to be reliable characters. However, *Enteromorpha ramulosa* had fewer pyrenoids per cell in cultured material than in collected specimens, and cultures of *E. prolifera* had more pyrenoids per cell than were common in collected material. *Enteromorpha clathrata* cells in culture were generally shorter in surface view than those in herbarium specimens, and *E. flexuosa* cells were typically longer in culture than those in collected material.

Despite these minor differences, the results of these cultural studies indicate that the eight species of Ulvaceae from Port Aransas maintain their normal cellular morphology in culture, that cellular characters are constant and reliable taxonomic criteria, and that cultural studies can aid in delimiting these species.

3. Studies of Growth in Culture

The results of the cultural studies discussed above indicated that it was generally possible to obtain plants with normal morphology in culture. However, *Ulva lactuca* and *Enteromorpha lingulata* both developed slowly and produced stunted fronds. No reason was readily apparent for the disparity of results for different species grown under uniform conditions. Therefore, an attempt was made to determine the basic factors responsible for normal thallus development.

Cultural conditions were the same as those used for the life-history studies. *Enteromorpha clathrata* and *Ulva fasciata* were used because of their demonstrated ability to grow normally and rapidly in culture. It seemed best to use species which could grow normally in culture so that a failure of fronds to develop under particular experimental conditions would be a reflection of the inadequacy of a certain set of conditions rather than a confirmation that a particular species was not well suited to the culture-chamber environment.

a. Axenic Cultures

Axenic germlings of both species were obtained by the spray-plate technique described by Wiedeman, Walne, and Trainor (1964). Purity of cultures was checked by inoculating 1% Bacto-Nutrient Agar plates (prepared with filtered seawater instead of distilled water) and incubating them under standard conditions for 72 hr. Axenic material was inoculated into cotton-plugged 50-ml Erlenmeyer flasks containing 40 ml of medium. Experiments were set up in duplicate and observed for a period of six weeks.

Initially, an attempt was made to grow axenic germlings of *Enteromorpha clathrata* in Ott's (1966) defined seawater. This synthetic medium consists of inorganic salts and lacks vitamins and known growth regulators. The germlings were unable to grow in this medium. Previous attempts to grow unialgal, but bacterized, germlings in the same medium had also failed. Therefore, new media were prepared by adding various known substances to Ott's medium to see if normal growth could be obtained.

Provasoli (1958) reported increased growth of *Ulva lactuca* in artificial seawater enriched with vitamins. Therefore, a medium was prepared by modifying Ott's medium with the addition of vitamin B_{12} (50 ug/1) and Eagle's vitamins (5 ml/1), which contain the following vitamins in the proportions listed: 0.5 mg/1 each of biotin, chlorine, floric acid, nicotinamide, pantothenic acid, pyridoxal, and thiamine; 0.05 mg/1 riboflavin; and 0.9 mg/1 inositol·$2H_2O$ (Eagle 1955). The *Enteromorpha clathrata* germlings again showed no detectable response to this new medium.

Finally, a medium was made from a combination of Ott's artificial seawater and von Stosch's (1964) enrichment as cited by Ott (1966) by preparing von Stosch's enrichment with Ott's medium substituted for filtered seawater. There was some growth in this medium, but germlings were covered with uniseriate filaments which produced a mold-like green colony (Fig. 105). This phenomenon was reported for axenic cultures of *Ulva lactuca* by Provasoli and Pintner (1967).

In all of these experiments, the plants remained green but generally failed to grow. Occasional erect filaments 5–10 mm in length appeared but failed to develop further (Fig. 107). Rhizoids typically proliferated forming a mycelium-like mat (Fig. 108). These results are apparently similar to those of Provasoli (1964) in his work with *Ulva lactuca*.

Levring (1946), Føyn (1960) and Provasoli (1964) have reported that artificial media now available are entirely inadequate for growing *Ulva*. These same authors obtained better growth for *Ulva* in seawater enrichments than in artificial media. Therefore, an attempt was made to grow axenic *Enteromorpha clathrata* germlings in filtered seawater enriched according to von Stosch (1964). Growth was no better in this medium than in Ott's.

Increased growth has been reported for *Ulva* in media enriched with IAA (indole-3-acetic acid) by Kylin (1942) and with adenine and kinetin by Provasoli (1958, 1964). However, von Stosch's enrichment fortified with adenine (30 mg/1) and kinetin (0.2 mg/1) had no obvious effect on germling growth. This was not surprising, since Provasoli obtained near-normal morphology (flat blades 2–3 cm long) for *Ulva lactuca* with media made from only one particular sea-

water sample; his results were not reproducible using other seawater samples.

An attempt was made to grow axenic *Ulva fasciata* germlings in filtered seawater enriched according to von Stosch (1964). Plants did not develop beyond the germling stage and invariably formed a green rhizoidal mass (Fig. 108). It was noted that occasional germlings developed into normal blades. When this occurred, a purity check made by transferring a drop of the suspect medium to Bacto-Nutrient Agar made with seawater always confirmed that the medium was contaminated with marine bacteria or marine yeasts. No attempt was made to identify these microorganisms. However, they were utilized in the following manner. Medium from flasks in which unialgal, but contaminated (bacterized), *Ulva fasciata* plants were growing normally was transferred to flasks containing stunted axenic germlings. This inoculum did not induce growth if the germlings had been axenic for more than two weeks and if they had produced a rhizoidal mass. Germlings would respond to the influence of this bacterized culture only during the initial period of germling development. Similar results were reported by Provasoli and Pintner (1964) in *Monostroma oxyspermum*. These authors concluded that the chemical symbiosis between marine algae and microorganisms is not restricted to nutrient exchange but apparently includes morphogenetic factors as well.

Many authors, including Kylin (1941, 1942). Levring (1946), Provasoli (1958, 1964), Føyn (1960), Nasr *et al.* (1968) and Berglund (1969a,b), have investigated the conditions necessary for culturing the Ulvaceae. In general, the published results of these investigations are in close agreement with the findings here reported. Berglund (1969a) domonstrated that organic substances excreted by *Enteromorpha linza* could be used to stimulate growth of axenic cultures of two species of *Enteromorpha: E. linza* and an unidentified species other than *E. linza*. Berglund (1969b) used axenic cultures of *Enteromorpha linza, Enteromorpha* sp. and *Cladophora gracilis* to determine the best source and optimum concentration for nitrogen, phosphorous, calcium, and halides in the artificial seawater ASP 6F. Both of these reports indicated that it is possible to increase growth in axenic cultures by carefully regulating environmental conditions and supplying nutrients and organic growth stimulators. However, normal frond morphology was not indicated for axenic cultures in either of these reports. Apparently, much detailed and systematic research remains before axenic cultures of Ulvaceae can be made to produce fronds with normal morphology.

b. Unialgal Cultures

An attempt was made to enhance the growth of unialgal *Ulva lactuca* in an enriched medium. Nasr *et al.* (1968) reported that urea increased growth of *Ulva* in culture. Von Stosch's enrichment was further enriched with urea (0.25 g/l) as suggested by these authors. Initially, *Ulva lactuca* plants in this experimental medium appeared to be larger and darker green than the control plants in von Stosch's enrichment. However, within three weeks, these fronds became intestiniform, bulbous, and contorted (Fig. 106). This urea-enriched medium was unsuitable for long-term maintenance of *Ulva lactuca* cultures.

4. Studies on the Effects of Salinity

The eight species of Ulvaceae observed in the vicinity of Pt. Aransas were limited to intertidal habitats. Such an environment is characterized by drastic salinity fluctuations which have a profound effect on the morphology and distribution of marine algae (Klugh, 1922; Gunter 1961; Munda 1966).

Salinity variations may have been responsible for some of the distributional patterns observed during this investigation. For instance, *Ulva fasciata* was collected exclusively on the southwest jetty at Pt. Aransas where the salinity fluctuates less than in the bays. Cauro (1958) reported that gametes of *U. fasciata* have a narrow tolerance of salinity changes. Obviously, such a restriction on the survival of reproductive bodies could be of prime importance in determining where germlings develop. Lersten and Voth (1960) found that an undetermined species of *Enteromorpha* in culture discharged swarmers more abundantly if the sporulating plants were maintained in seawater of normal salinity (33‰). They reported a reduction of reproductive capacity for plants in dilute and hypersaline seawater.

In some instances salinity variations may be responsible for vertical distribution and seasonal periodicity of marine algae. Waern (1957) reported that *Enteromorpha intestinalis* and *E. compressa*, both littoral-zone species elsewhere, descended to 7–8 m in the hyposaline Baltic Sea. Boyle and Doty (1949) found experimentally that *Sphaerotrichia divaricata* and *Fucus vesiculosus*, both stenohaline algae, could tolerate dilute seawater if the water temperature was reduced. This phenomenon may provide an explanation for the occurrence of stenohaline forms in brackish water during winter. It may also be the reason for the winter growth peak of the Ulvaceae in the Texas bays which were hyposaline during this study.

Salinity has been cited as the cause of polymorphism in the Ulvaceae. Klugh (1922) found that *Enteromorpha clathrata* growing in a salinity of 22‰ was highly branched and had short, monosiphonous branch tips. This same species growing in salinities of 1–3‰ was sparsely branched and superficially resembled *Ulothrix*. Arasaki and Shihira (1959) found morphological variations in *Enteromorpha linza* which were correlated with environmental factors, including salinity.

An analysis of algal specimens collected during this investigation showed a wide degree of variation in morphological characters for most species. Because of these results and the reports of workers such as Klugh (1922) and Arasaki and Shihira (1959), an attempt was made to determine if different salinity regimes would produce a change of plant morphology in culture.

a. Materials and Methods

Filtered seawater with an initial salinity of 31‰ was variously diluted and concentrated to produce separate aliquots of seawater with salinities of 5, 15, 25, 35 and 45‰. Dilution was accomplished by adding a predetermined volume of distilled water to the individual seawater aliquots. Hypersaline solutions were prepared by first doubling the concentration of salts in a measured amount of sea-

water by boiling and then adding this concentrated solution to seawater with a salinity of 31‰ until the desired salinity was achieved. The resulting salinities were tested with a Goldberg Refractometer (Behrens 1966) and enriched according to von Stosch (1964).

Fifty-ml-capacity Petri dishes containing 40 ml of medium were used in this experiment. The Petri dishes were illuminated with 50 ft-c indirect light from 40-W Ken-Rad "Cool White" fluorescent bulbs in a culture chamber with a 24-hr cycle of 12-hr light and 12-hr dark.

Seven-day-old germlings approximately 1 cm long were inoculated into the Petri dishes simultaneously. The eight Texas species of Ulvaceae were used in this experiment. Since sexual dimorphism had appeared in some species during the previous cultural studies, gametophytes of both sexes were used when available. Both male and female gametophytes of *Enteromorpha salina*, *E. clathrata*, *E. lingulata*, *E. prolifera*, and *Ulva lactuca* were used, while only sporophytes were available for *Enteromorpha flexuosa*, *E. ramulosa*, and *Ulva fasciata*.

Two germlings were placed in each Petri dish and two Petri dishes were used for each of the gametophytes or the sporophyte representing each species. This set-up was duplicated so that two Petri dishes were used for all of the plants for each species in all five salinity regimes.

The cultures were maintained under a low light intensity of 50 ft-c to prevent sporulation, as suggested by Lersten and Voth (1960). Thus, it was possible to make an assessment of vegetative growth. After 32 days, fronds were measured and their growth compared. At that time, the light intensity was increased to 200 ft-c incident light so that sporulation could occur. Plants were maintained in this more intense light for ten days and then observed for evidence of sporulation, i.e., germling development. This experiment was terminated after 42 days. The media were then tested and the salinities were found to be 10, 20, 30, 45 and 55 ‰.

b. Results

The results of this study are summarized below for the different taxa:

Ulva lactuca (Figs. 113, 114)

Both male and female gametophytes developed poorly in all salinity regimes. Growth seemed best in a salinity of 50 ± 5 ‰. There was no evidence of sexual dimorphism or of sporulation in these cultures. These results are somewhat surprising, since *Ulva lactuca* is generally associated with brackish water (Doty and Newhouse 1954) and was found most commonly in this study in the hyposaline Aransas Bay. The growth response of this species may be a reflection on its inability to develop normally in culture rather than the relative suitability of different salinities.

Ulva fasciata (Fig. 115)

Sporophytes of this species developed best in a salinity of 40 ± 5 ‰. Growth was reduced in higher and lower salinity concentrations. No sporulation was observed, but this was probably due to the immaturity of the plants.

Microscopic examination of this material showed normal cellular morphology in plants from salinities of 40 ± 5 and 50 ± 5 ‰ (Fig. 127, 128). Cells from plants in salinities of 27.5 ± 2.5 and 17.5 ± 2.5 ‰ had abnormally large vacuoles and were of many different sizes (Figs. 125, 126). Cells from plants in the 7.5 ± 2.5 ‰ salinity regime were completely abnormal and possessed large vacuoles and a spherical, rather than angular, cell outline (Fig. 124).

These results are in agreement with field studies which indicated the *Ulva fasciata* is much less euryhaline than other species observed.

Enteromorpha flexuosa (Fig. 120)

Sporophytes of this species grew best in a salinity of 50 ± 5‰. Growth was good in 40 ± 5‰, but not as luxuriant as in 50 ± 5‰. Sporulation occurred in all salinity regimes but was best in 17.5 ± 2.5 and 27.5 ± 2.5‰.

Enteromorpha ramulosa (Fig. 121)

Sporophytes developed well in salinity concentrations of 25–55‰. Sporulation occurred in all salinity regimes and was heaviest in 15–45‰.

Enteromorpha clathrata (Figs. 109, 110)

Gametophytes of both sexes developed best in a salinity of 27 ± 2.5‰. The male plants seemed to develop in all salinities, while female plants were generally stunted in all but the 27.5 ± 5‰ regime. Sporulation was best for gametophytes of both sexes from 15–30‰.

Enteromorpha salina (Figs. 116, 117)

Plants of this species were markedly sexually dimorphic. Female gametophytes were small and stunted with best growth occurring in a salinity of 17.5 ± 2.5‰. Male gametophytes developed large normal fronds in salinities of 25–55‰. The female plants sporulated best at 27.5 ± 2.5‰, while the males sporulated best between 35–55‰.

Microscopic examination of male gametophytes showed abnormal frond morphology in plants from reduced and concentrated salinities. Fronds in 7.5 ± 2.5 salinity developed solid cellular protrusions resembling stunted branchlets (Fig. 122). Fronds in 50 ± 5‰ produced short, uniseriate filaments of large-vacuolated cells (Fig. 123). This profusion of filaments gave the fronds a fuzzy appearance similar to the mycelial-like masses which developed in axenic cultures of *Enteromorpha clathrata.*

Enteromorpha prolifera (Figs. 111, 112)

Both male and female gametophytes of this species developed well in all salinity regimes. The male plants were largest and more abundantly branched in a salinity of 40 ± 5‰. The females were largest in 40 ± 5‰ but more abundantly branched in 50 ± 5‰ seawater. Plants were not noticeably sexually dimorphic

except that branching for male and female gametophytes was most abundant in different salinity regimes. Previous culture studies in normal seawater (32‰) indicated that the male gametophytes were more abundantly branched than the female. These latter data seem to indicate that plants of both sexes have an equal ability to branch, but that different environmental conditions promote branching for male and female plants.

Sporulation occurred in 25–45‰ for plants of both sexes.

Enteromorpha lingulata (Figs. 118, 119)

Plants of this species were markedly sexually dimorphic. The female gametophytes were small and stunted in all salinities of 25–45‰.

Sporulation occurred in all salinities but was best for male plants in 27.5 ± 2.5‰ salinity and for females in 35–55‰.

c. Discussion and Conclusion

The results of this study agree with the findings of other workers who have reported that the Ulvaceae are, in general, euryhaline (Rea 1964, Bernstein 1967). Furthermore, Kylin (1938) and Biebl (1962) reported that some members of the Ulvaceae have very wide salt tolerances and can withstand temporary variations of 0.2 to 3.0 times normal salinity.

It is interesting to note that three of the four *Enteromorpha* species which reproduce by an alternation of gametophytic and sporophytic generations demonstrated sexual dimorphism in this study. In *Enteromorpha salina* and *E. lingulata*, the female plants were stunted, while male plants developed large fronds, usually in slightly higher salinity concentrations than the female gametophytes. In *E. prolifera*, the gametophytes of both sexes developed large fronds in the same salinity concentrations, but branching was most abundant in different salinity regimes for male and female plants. *Enteromorpha clathrata* was the only species with an alternation of sexual and asexual generations which demonstrated a uniformity of morphology for plants of both sexes in the different regimes.

The two species which lack a sexual phase, *Enteromorpha flexuosa* and *E. ramulosa*, both developed best in a salinity of 50 ± 5‰. Curiously, they seemed to reproduce in the lower salinity concentrations which were less favorable for growth. This same tendency was noted in other species, notably *E. prolifera* and *E. salina*, and may represent a survival mechanism which induces sporulation when conditions are unfavorable for growth.

As mentioned above, *Ulva lactuca* did not grow well in any salinity regime. *Ulva fasciata* developed well in a salinity of 40 + 5‰, but not in lower concentrations. *Ulva fasciat*a seemed to be much less euryhaline than the other species observed.

The results of this investigation have helped to explain the polymorphic nature of the Ulvaceae, especially among the species of *Enteromorpha*. Most species demonstrated a gradation of branching of male and female gametophytes which differed in the various salinity regimes. If this phenomenon occurs in nature, male and female plants of the same species would appear differently under a

salinity regime and, consequently, a vast gradation of morphological forms would appear for each species depending on the salinity.

Finally, this study indicated that species of *Enteromorpha* tend to be more highly branched in media with higher salinity and less abundantly branched or even unbranched in dilute salines. These results are in agreement with Klugh's (1922) observations of plants in nature.

5. Cytological Studies

Chromosome counts were made for the eight Texas species of Ulvaceae to confirm the presence of alternating haploid and diploid phases of *Entermorpha* and *Ulva* and to elucidate any specific relationships between chromosome number and morphology. Similar studies with these genera have been conducted by other workers. The presence of haploid and diploid generations has been reported in *Ulva lactuca* (Føyn 1929, 1934) and in *Enteromorpha compressa* (Ramanathan (1936), Levan and Levring (1942), Niizeki (1957, cited by Bliding, 1963), Sarma (1958, 1959) and Yabu and Tokida (1960) have conducted cytological investigations of various species of Ulvaceae.

a. Materials and Methods

Plants for this study were grown under standard conditions. The photoperiod of 12-hr was found adequate for synchronizing mitotic divisions, although it was different from that recommended by Løvlie (1964) for *Ulva lactuca*. Two-week-old plants were used routinely because their cells were actively undergoing vegetative divisions and were not obstructed with starch granules, as was the case in the cells of older plants.

Several different staining techniques were tried before a satisfactory method was found. Initially, an acetocarmine stain as described by Cave and Pocock (1951) was tried. Although this method stained vegetable nuclei clearly, it gave poor results with chromosomes. A Feulgen stain used successfully by Dube (1967) for *Monostroma* was tried and similarly proved to be inadequate for staining chromosomes. Next, an aceto-carmine technique for using an ethanolacetic acid fixative as recommended by Bischoff (1959) was tried unsuccessfully. Finally, a satisfactory technique was found based on the methods used by Godward (1948) and Buffaloe (1958). Plant material was fixed in an I_2KI-formalin solution (Buffaloe 1958) during the middle of the dark cycle. This material remained in the fixative for at least 12 hr, was then washed thoroughly in distilled water and then placed in an iron-alum mordant (Godward, 1948). *Enteromorpha* material was soaked in the mordant for 5 min, but a 1-min soak was adequate for *Ulva*. After another thorough rinse in water, the material was stained in aceto-carmine (Cave and Pocock 1951) for at least two hr but was not heated as suggested by Buffaloe (1958).

b. Results

In general, the results of this cytological investigation agreed with the reports

by other workers. Mitotic divisions were cyclic and photoperiod-regulated. Material fixed during the light period seldom contained dividing cells, while material fixed during the middle of the dark period contained the greatest number of mitotic divisions. Løvlie (1964) reported that cells in *Ulva mutabilis* divided during the middle of the dark period and had a generation time which was a multiple of 24 hr. Thus, divisions occurred at 24-hr intervals, but by no means did all cells divide every day. Bråten and Løvlie (1968) confirm this observation in their ultrastructural study of this same species.

The interphase nucleus for all species had a diameter of 3–4 μ. The nuclear membrane disappeared before metaphase and reappeared during the formation of daughter nuclei. Exact chromosome counts were difficult because of their small size (0.5–1.5 μ) and because of the appearance of a large number of chromatin granules during early prophase. Dangeard (1899, cited by Buffaloe, 1958) and Kater (1929) reported difficulties in making chromosome counts in *Chlamydomonas* because of similar chromatin bodies. These chromatin bodies condensed into chromosomes by late prophase. Chromosome counts were made during metaphase when the chromosomes were arranged in a circle and were most distinct, especially in polar view. Whole mounts were used for these counts instead of squashes, so that the stage of division could be accurately determined; otherwise, prophase chromatin bodies could have been mistaken for metaphase chromosomes. All chromosomes appeared to be of equal size and identical shape so that no distinction could be made. Nucleoli which had disappeared during prophase reappeared during telophase just before the nuclear membranes formed around the groups of daughter chromosomes. No centrioles or spindle fibers were observed in this study.

Ten metaphase chromosomes were observed in vegetative gametophytic material of *Ulva lactuca, U. fasciata, Enteromorpha, clathrata, E. lingulata, E. salina, E. prolifera* (Figs. 129–144) and in sporophytic material of *E. flexuosa.* Twenty metaphase chromosomes were observed in *E. ramulosa* and in sporophytic material of *E. salina* and *U. fasciata* (Figs. 131, 132, 139, 140, 144).

These results indicated that the typical haploid chromosome number of the local Ulvaceae is 10. The occurrence of 20 chromosomes in vegetative cells of sporophytes of *Ulva fasciata* and *Entermorpha salina* indicated that these two species, and probably other sexually reproducing ones, have an alternation of haploid and diploid phases. The count of 20 chromosomes in *Entermorpha ramulosa* and of 10 chromosomes in *E. flexuosa* demonstrated that asexually reproducing species are not necessarily always diploid. It would be interesting to conduct further studies to determine if the respective chromosome numbers of 10 and 20 for *E. flexuosa* and *E. ramulosa* are conserved from generation to generation. It would also be interesting to know if the races of *E. prolifera* which reproduce by the sequential production of bi- and quadriflagellate swarmers have a haploid, diploid, or fluctuating chromosome number.

Although sporophytes tend to be diploid and gametophytes tend to be haploid, variations do occur. The occurrence of haploid and diploid chromosome numbers in otherwise *bona fide* sporophytes is in agreement with Føyn's (1962) observation that there is no causal relationship between the alternation of generations

and the alternation of haploid and diploid phases. Føyn (1962) further reported the occurrence of diploid gametes in size and behavior except that they were unable to copulate.

It is perhaps significant that the chromosome number for all the local species of Ulvaceae was 10 to 20. Similar studies on the Ulvaceae elsewhere have led to reports of highly variable chromosome counts. For instance, *Ulva lactuca* has been reported to have a haploid count of 10 (Carter 1926; Sarma 1959) and 13 (Føyn 1929, 1934; Levan and Levring 1942). *Enteromorpha compressa* has been reported to have a haploid count of nine (Sarma 1958) and ten (Ramanathan 1936, 1939). Other species of *Entermorpha* have been reported to have disparate numbers of chromosomes: *E. linza* with 12 (Niizeki 1957, cited by Bliding 1963), *E. ramulosa* with 12 (Sarma 1958) and *E. intermedia* with 16 (Sarma 1958).

The disparity of results among workers could be the result of faulty counts based on chromatin bodies instead of chromosomes, or the occurrence of races with different chromosome numbers for certain species. Godward (1966) reported that aneuploidy was significantly more common than polyploidy in the Ulotrichales. It is possible that the chromosome counts of 9–16 are accurate and reflect the occurrence of races as well of species which are genetically distinct.

c. Discussion and Conclusions

The chromosome number for all the Texas species of Ulvaceae was 10 or 20. The chromosome count of 20 for *Enteromorpha ramulosa* is presumed to be diploid and thus the haploid number for all the species is 10. This identical chromosome count for all the species would seem to indicate that they are more homogeneous than are similar groups of species of Ulvaceae studied in other areas. Also, the local species with an alternation of gametophytic and sporophytic generations also seem to have an alternation of haploid and diploid phases. However, life history phases cannot be correlated arbitrarily with either a haploid or diploid nuclear condition.

6. Hybridization Studies

An investigation was made of the interbreeding behavior of the six sexually reproducing species of Ulvaceae on the Texas coast. According to Føyn (1955) and Bliding (1955, 1963, 1968), the intersterility of sexually reproducing Ulvaceae is the best criterion for specific delimitation. Thus, failure or ability of the isolates in this study to hybridize and to produce viable zygotes would reflect on the validity of the previous taxonomic designations which were based on morphological considerations.

a. Materials and Methods

Male and female gametophytes of *Ulva lactuca, U. fasciata, Enteromorpha clathrata, E. lingulata, E. prolifera* and *E. salina* were induced to release gametes simultaneously by placing mature fronds into fresh medium, as described by Lersten and Voth (1960) and Thiadeus and Zeuthen (1967). Mature plants

typically released gametes on both the second and third days after the medium had been changed.

Male and female gametes of both *Ulva* species were mixed as were gametes of both mating types for all four *Enteromorpha* species. Male and female gametes of both *Ulva* species were also mixed with gametes of both mating types of *Enteromorpha lingulata.*

b. Results

In all cases, mixtures of male and female gametes demonstrated clumping, pairing and plasmogamy similar to the reproductive behavior of mixtures of male and female gametes of the same species. However, noticeably fewer gametes in mixtures from different species were involved in this reproductive behavior than were gametes in mixtures from the same species.

Gamete mixtures which had been formed on glass slides were pipetted into 50-ml Petri dishes and observed periodically. Within seven days, two types of germlings were visible in all of the Petri dishes. It was not possible to determine if these germlings were sporophytes or parthenogenetic gametophytes. Earlier developmental studies had shown that sporophytes and male gametophytes were similar to each other and distinct from female gametophytes. However, after 14 days, examination of the Petri dishes revealed that three different gamete mixtures contained germlings of a type previously unobserved (Figs. 145–148). These germlings were Y-shaped, and consisted of an erect filament supported by two basal rhizoidal systems separated from each other and joined to the basally dichotomous erect filament. These distinctive germlings were found in Petri dishes containing mixtures of male gametes from *Enteromorpha lingulata, E. prolifera, E. clathrata* and female gametes of *E. salina.*

After 21 days, 10 plants were removed from each Petri dish and were placed in individual Petri dishes of fresh medium so that sporulation would occur. Most *Enteromorpha* fronds originating from mixtures of male and female gametes from the same species produced quadriflagellate zoospores and were thus considered to be sporophytes. A few parthenogenetic gametophytes were isolated from these same mixtures.

The Y-shaped fronds produced both bi- and quadriflagellate swarmers simultaneously. This phenomenon had not been observed before in any culture during the investigation. There was a tendency for these fronds to produce a greater proportion of biflagellate swarmers on the second day after swarmer induction, and then to produce a greater proportion of quadriflagellate swarmers on the third day.

Fronds originating from all other mixtures of gametes from *Ulva* and *Enteromorpha* species proved to be gametophytes. Of course, mixtures of male and female gametes of *Ulva lactuca* and of gametes of both sexes of *U. fasciata* resulted in sporophytes which produced quadriflagellate zoospores.

Fronds of all three putative hybrids were examined microscopically. Cellular characters such as size, shape, and dimensions were in all cases in agreement with cultural material of *Enteromorpha salina* gametophytes. None of these cellular

characters was found to be in specific agreement wtih the gametophytes of the other three species.

Finally, fronds from all three putative hybrids were fixed and stained in accordance with the techniques outlined for the previous cytological study. Results of this investigation indicated that all the material observed for all three suspected hybrids had a chromosome number of 10, apparently the haploid number (Figs. 149–151).

At first, the results of the investigations on the three putative hybrids seem contradictory. Cytological studies indicated that karyogamy had not occurred (the plants were haploid) and that the plants were identical to *Enteromorpha salina* instead of being intermediate as might have been expected of hybrids. However, developmental studies indicated that a new type of germling was present. Furthermore, the suspected hybrids produced both bi- and quadriflagellate swarmers.

Several explanations can be suggested to interpret these seemingly contradictory results. Jónsson (1967, 1968) reported that the life history of *Acrosiphonia* normally includes "micto-haploid" plants which are completely identical to gametophytes except that they initially have a peculiar 1N + 1N nuclear condition instead of the 1N condition of gametophytes or the 2N of the heteromorphic sporophytes. It is possible that plasmogamy, but not karyogamy, occurred between female gametes of *Enteromorpha salina* and made gametes of *E. prolifera*, *E. lingulata* and *E. clathrata*. However, it is unlikely that such a distinctive double nuclear condition would have been undetected in the cytological studies.

Føyn (1958) reported the simultaneous production of bi- and quadriflagellate swarmers in connection with 'progressive diploidization" in *Ulva mutabilis*. Gayral (1967) reported the same phenomenon in *Ulva fasciata* and *Enteromorpha flabellata*. Progressive diploidization would explain the occurrence of the haploid chromosome number in vegetative cells and the subsequent production of quadriflagellate zoospores in cells which underwent chromosome doubling during sporogenesis.

Another possibility is that some parthenogentic female gametophytes of *Enteromorpha salina* mutated. Gayral (1967) reported the spontaneous occurrence of a mutant from parthenogenetic gametes of *Ulva fasciata*. Such a mutant could be entirely similar to normal *Enteromorpha salina* female gametophytes, as were the suspected hybrids, except that they produced both bi- and quadriflagellate swarmers and had a distinctive germling stage.

An analysis of these incompatible results indicated that true hybridization involving plasmogamy and karyogamy of gametes from separate species could not have occurred. Apparently a phenomenon such as micto-haploidization, progressive diploidization, or mutation was responsible for the appearance of suspected hybrids.

c. Discussion and Conclusion

Ulva lactuca and *U. fasciata* were reproductively distinct from each other and from *Enteromorpha lingulata* and almost certainly from all other *Enteromorpha*

species. Mixtures of gametes of the four sexually reproducing *Enteromorpha* species were unable to form viable sporophytes. Evidently, strict intersterility barriers do exist between species of Ulvaceae as demonstrated by Bliding (1963).

SUMMARY AND CONCLUSIONS

Field and cultural investigations were conducted on the eight species of Ulvaceae occurring on the Texas coast in the vicinity of Port Aransas: *Ulva lactuca*, *U. fasciata*, *Enteromorpha clathrata*, *E. salina*, *E. lingulata*, *E. prolifera*, *E. ramulosa*, and *E. flexuosa*.

Keys and descriptions based on a synthesis of information from field specimens and from a literature survey are presented for the eight local species.

Field specimens were analyzed to determine the constancy of specific morphological characters such as frond length and width, degree of branching, and cellular dimensions.

Reproductive material for the eight species was collected and isolates of gametophytes and sporophytes were maintained in culture.

Different combinations of media, temperature, light intensity and photoperiod were utilized to determine which cultural conditions would support optimal growth.

Reproductive history and behavior of reproductive cells were determined for each species in culture. Three types of life cycles were noted in these isolates: (1) a diplobiontic isomorphic alternation between unisexual gametophytes and sporophytes; (2) absence of the sexual phase with reproduction by quadriflagellate zoospores; and (3) an alternation between sporophytic generations sequentially producing bi- and quadriflagellate zoospores.

Germination of zoospores, parthenogenetic gametes, and zygotes was observed in culture. All species were found to have one of two types of initial germling development. Germling type was found to be constant for both the sporophytes and gametophytes of individual species.

Isolates of all species were grown under uniform environmental conditions to determine the constancy of specific morphological characters. Frond shape, degree of branching, and cellular dimensions of cultured plants were observed to be fairly constant and to coincide with these characteristics of plants growing in the field. Also noted was a tendency for certain species to be sexually dimorphic in culture, the male gametophytes being larger and more highly branched than female gametophytes.

Ulva fasciata and *Enteromorpha clathrata* were grown axenically in several defined and enriched media. All attempts to elucidate minimum requirements necessary to permit normal development failed.

Male and female gametophytes and sporophytes were grown in media with salinities of $7.5 + 2.5$, 17.5 ± 2.5, 27.5 ± 2.5, 40 ± 5, 50 ± 5‰. Branched species were more highly branched in elevated salinities and nearly unbranched in low salinities. Different growth and reproductive responses were noted for male and female gametophytes of some species.

Cytological investigations revealed an alternation of haploid and diploid phases

in *Ulva fasciata* and *Enteromorpha salina*. A haploid chromosome number of ten was determined for all species.

Attempts at obtaining interspecific and intergeneric hybrids from the sexually reproducing *Ulva* and *Enteromorpha* species failed. Evidence for interspecific sterility was discussed and explanations given for the spontaneous appearance of a new germling type among the putative hybrids.

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FIG. 1–4

FIG. 1,2. *Ulva fasciata* collected at Pt. Aransas
FIG. 3,4. *Ulva lactuca* collected near Fulton harbor.

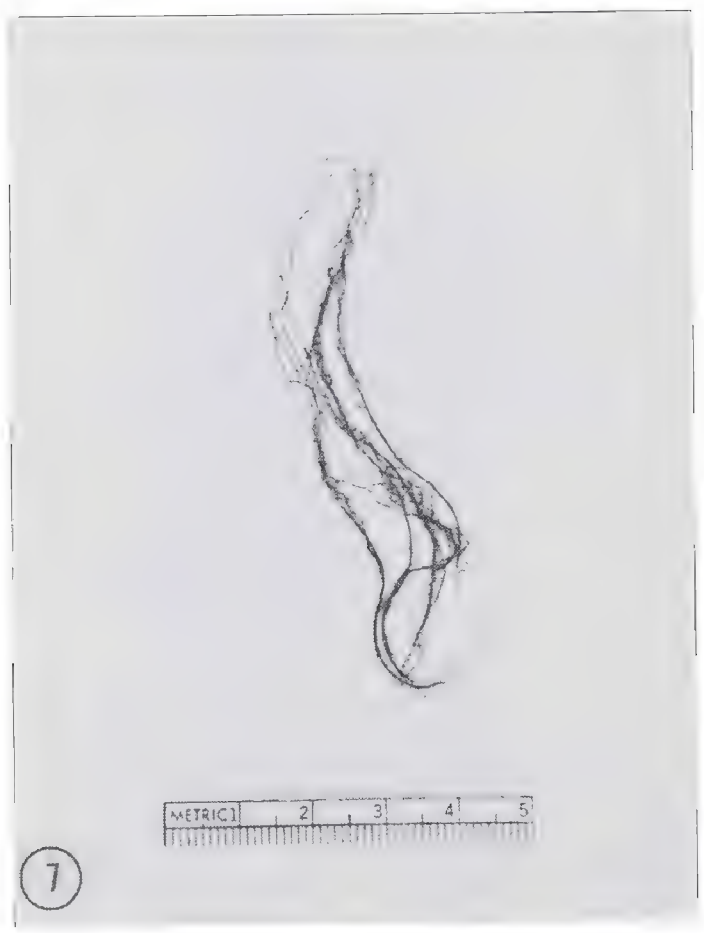


FIG. 5–8

FIG. 5,6. *Enteromorpha clathrata* collected at Pt. Aransas.

FIG. 7,8. *Enteromorpha ramulosa* collected at Pt. Aransas.

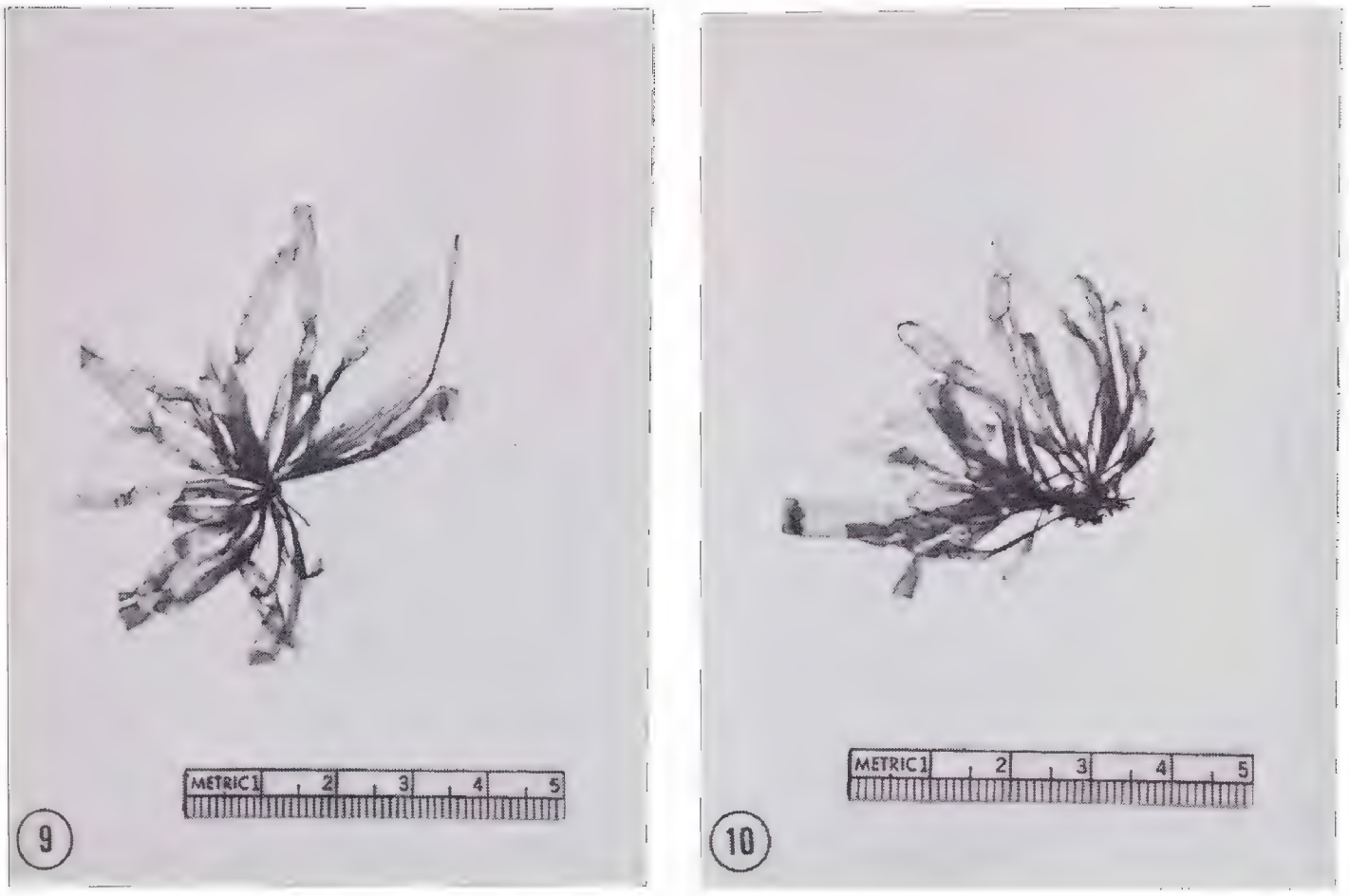


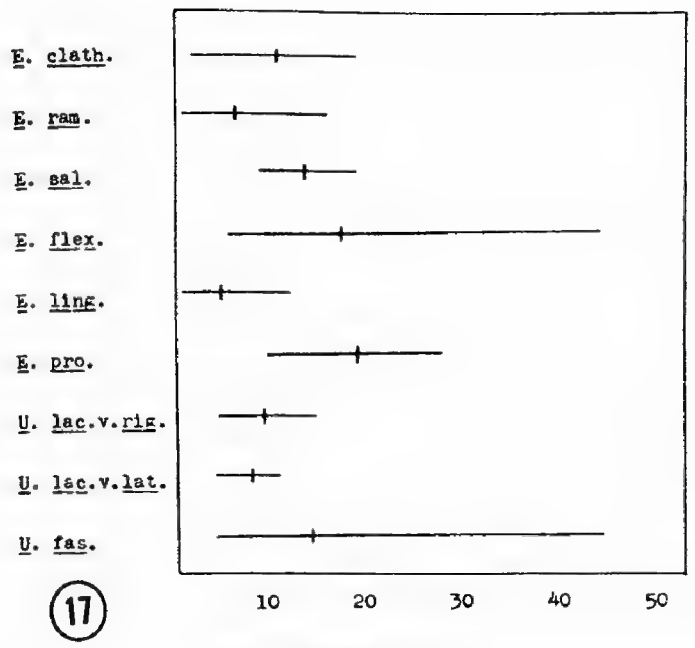
FIG. 9–12

FIG. 9,10. *Enteromorpha lingulata* collected at Pt. Aransas.
FIG. 11,12. *Enteromorpha salina* collected at Pt. Aransas.

FIG. 13–16

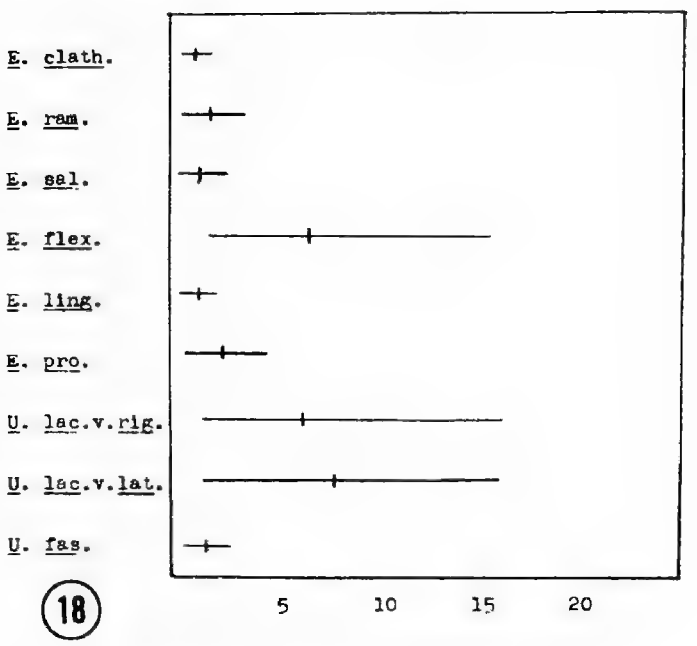
FIG. 13,14. Branched and unbranched specimens of *Enteromorpha flexuosa* collected near Fulton harbor.

FIG. 15,16. *Enteromorpha prolifera* collected at Pt. Aransas.



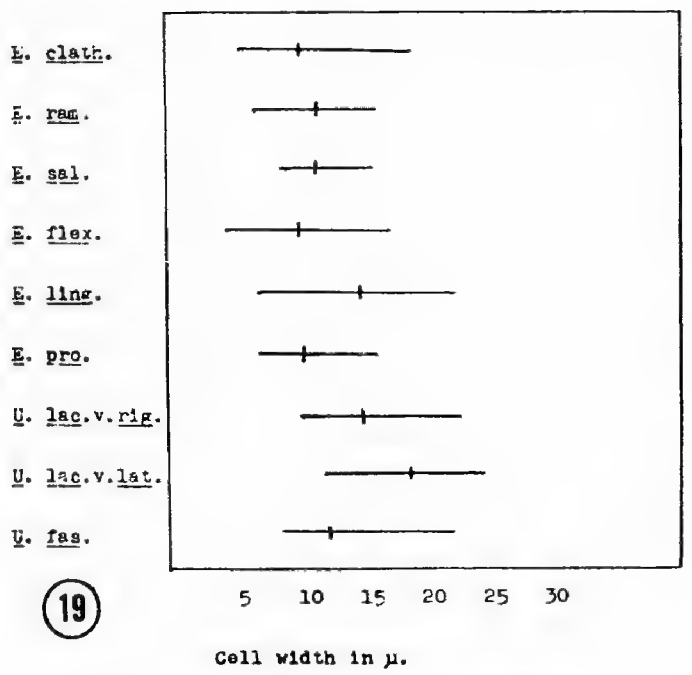
17

Frond length in cm.



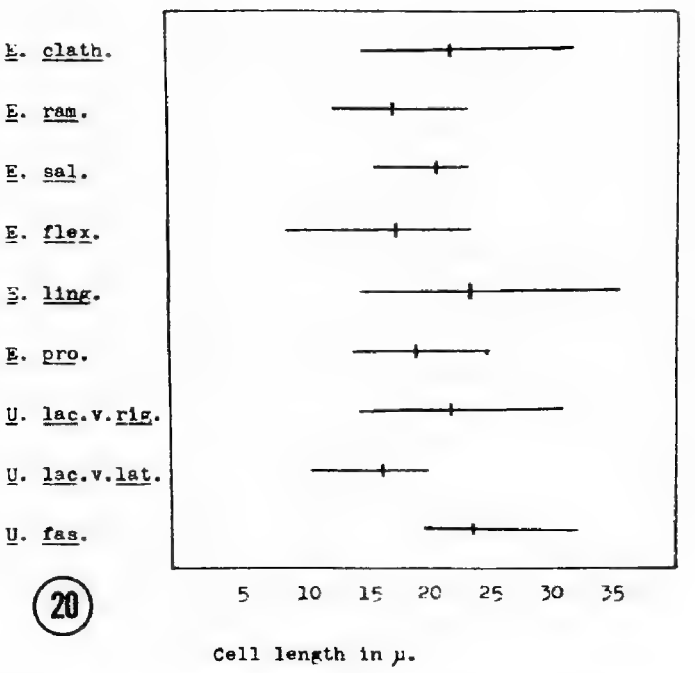
18

Frond width in mm (cm for Ulva species).



19

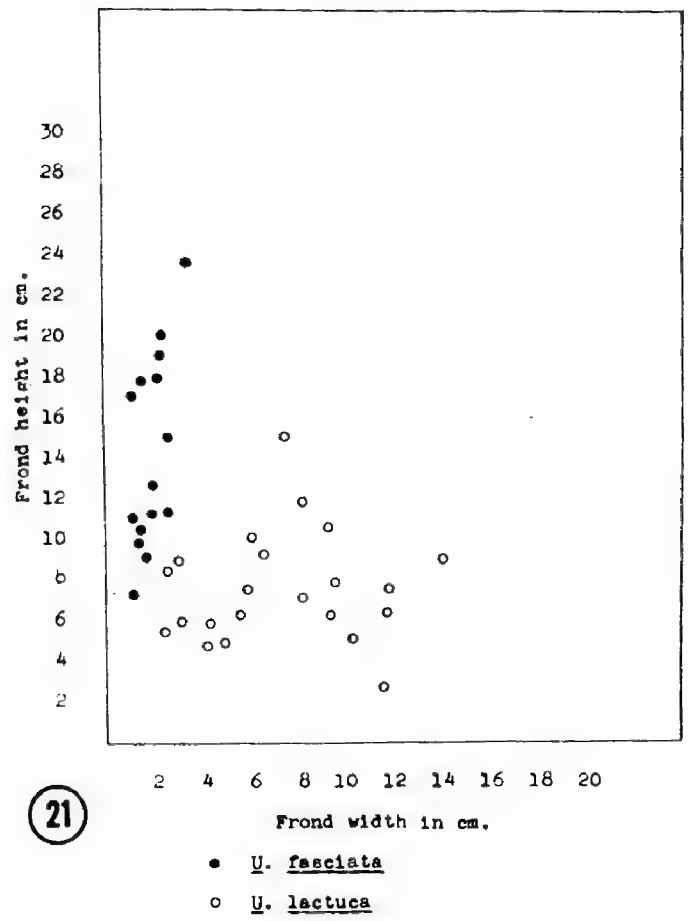
Cell width in μ.



20

Cell length in μ.

FIG. 17–20. Measurements of vegetative characters for the local Ulvaceae. Range is shown by vertical line, mean by horizontal bar.



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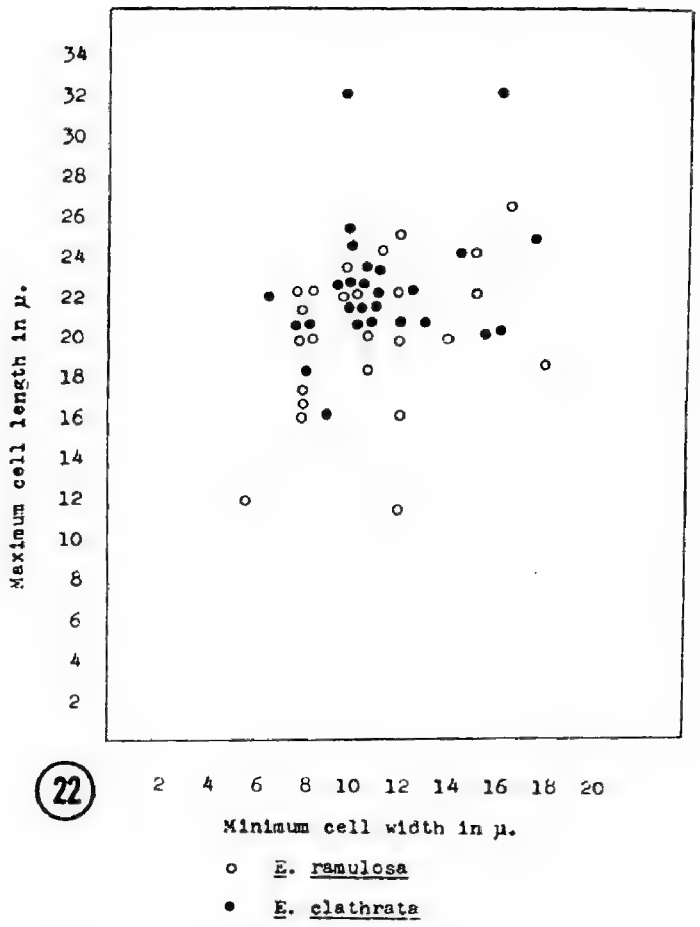

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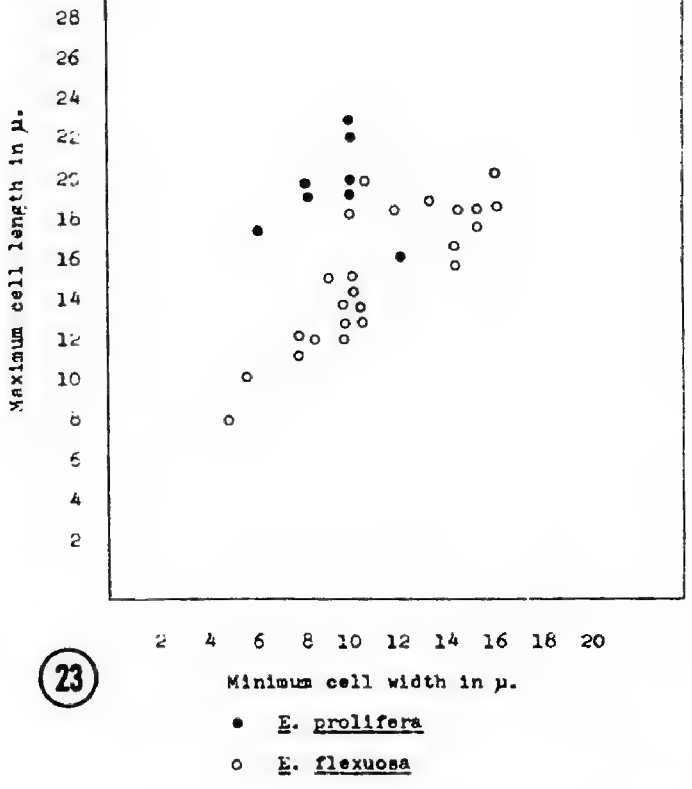

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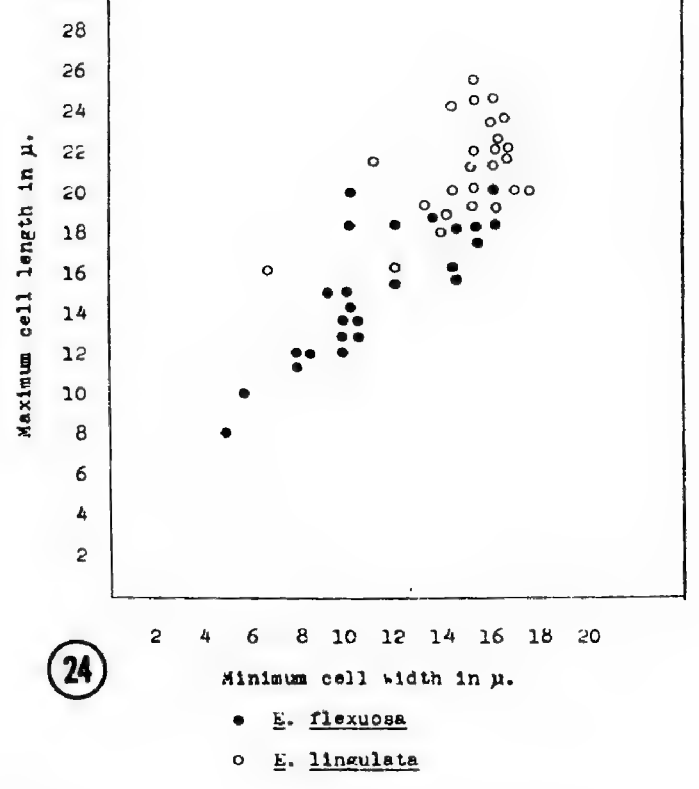
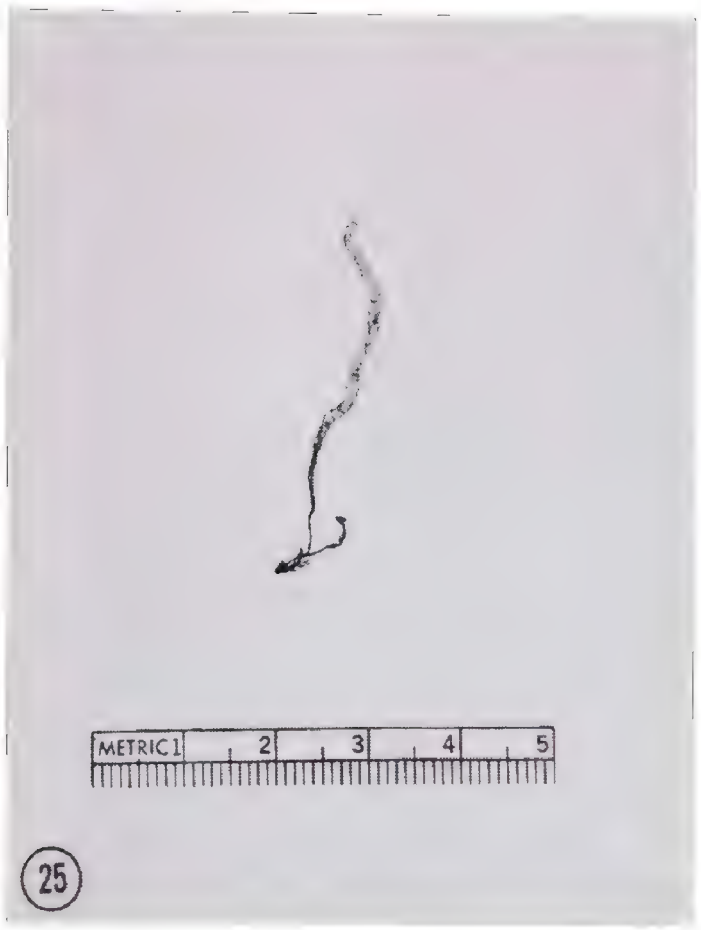


24

FIG. 21–24

FIG. 21. Measurements in cm for frond height and width in *Ulva fasciata* and *U. lactuca*.
FIG. 22. Measurements in μ for cell length and width in *Enteromorpha clathrata* and *E. ramulosa*.
FIG. 23. Measurements in μ for cell length and width in *Enteromorpha prolifera* and *E. flexuosa*.
FIG. 24. Measurements in μ for cell length and width in *Enteromorpha flexuosa* and *E. lingulata*.



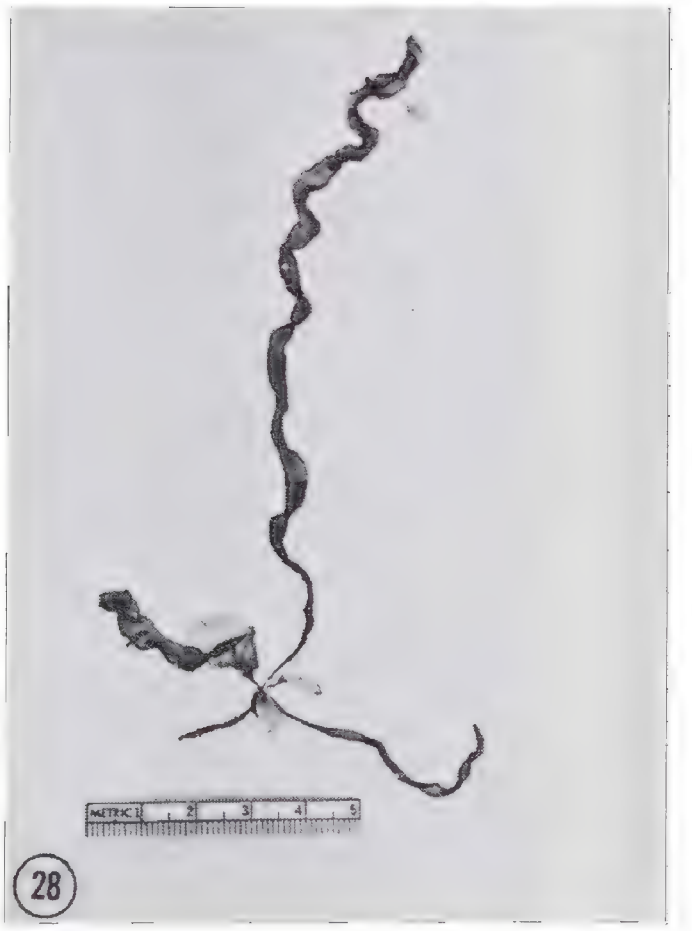


FIG. 25–28

Plants maintained in culture.

FIG. 25. *Ulva lactuca* 6-week old female gametophyte.

FIG. 26. *Ulva lactuca* 6-week old male gametophyte.

FIG. 27. *Ulva fasciata* 4-week old male gametophyte.

FIG. 28. *Ulva fasciata* 4-week old female gametophyte.

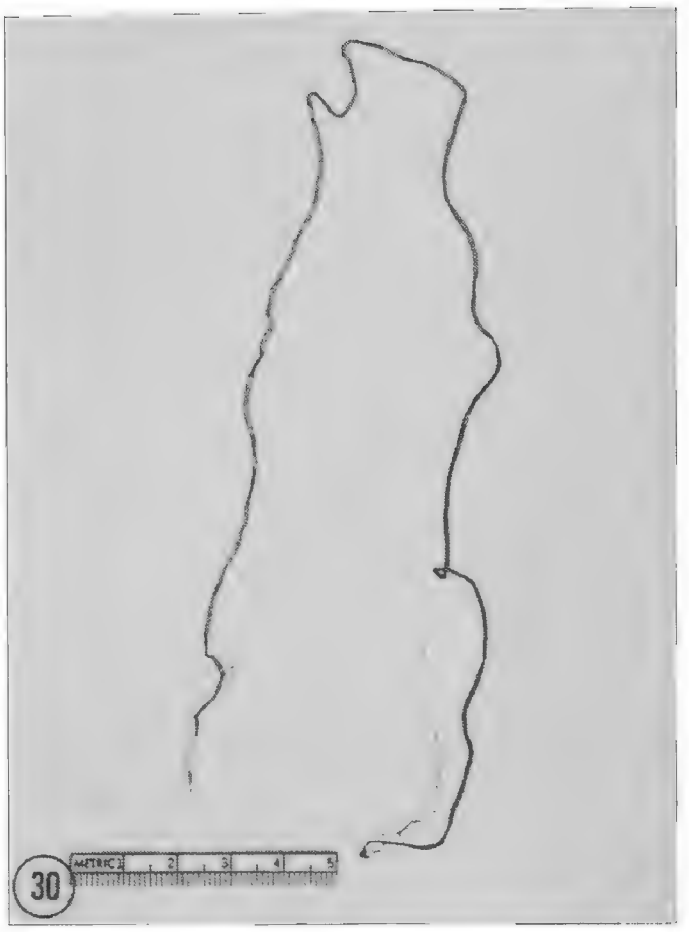


FIG. 29–32

Plants maintained in culture for 3 weeks.

FIG. 29. *Enteromorpha salina* male gametophyte.

FIG. 30. *Entermorpha salina* sporophyte.

FIG. 31. *Enteromorpha salina* female gametophyta.

FIG. 32. *Enteromorpha ramulosa* sporophyte.

FIG. 33–36

Plants maintained in culture for 3 weeks.

FIG. 33. *Enteromorpha prolifera* male gametophyte.

FIG. 34. *Enteromorpha prolifera* female gametophyte.

FIG. 35. *Enteromorpha prolifera* sporophyte producing biflagellate zoospores.

FIG. 36. *Enteromorpha prolifera* sporophyte producing quadriflagellate zoospores.

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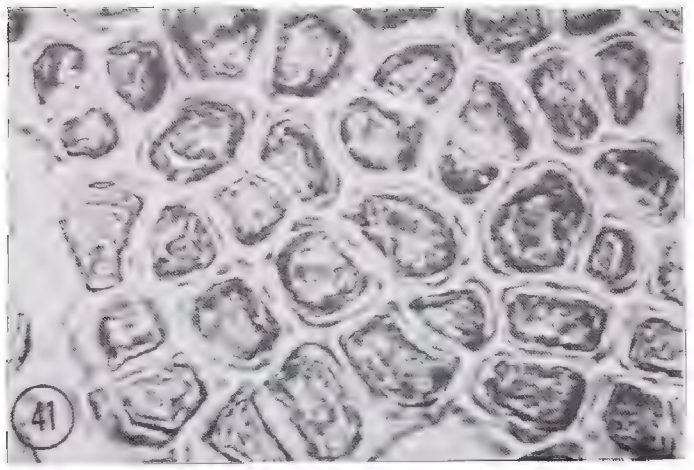
FIG. 37–40
Plants maintained in culture for 3 weeks.

FIG. 37. *Enteromorpha clathrata* female gametophyte.
FIG. 38. *Enteromorpha flexuosa* sporophyte.
FIG. 39. *Enteromorpha lingulata* female gametophyte.
FIG. 40. *Enteromorpha lingulata* male gametophyte.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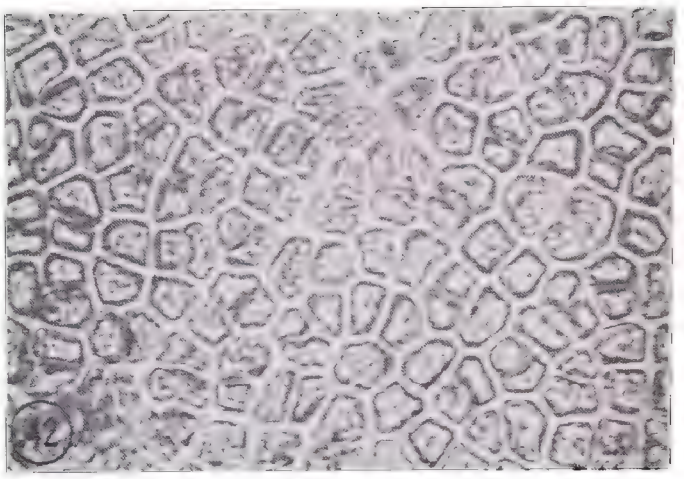
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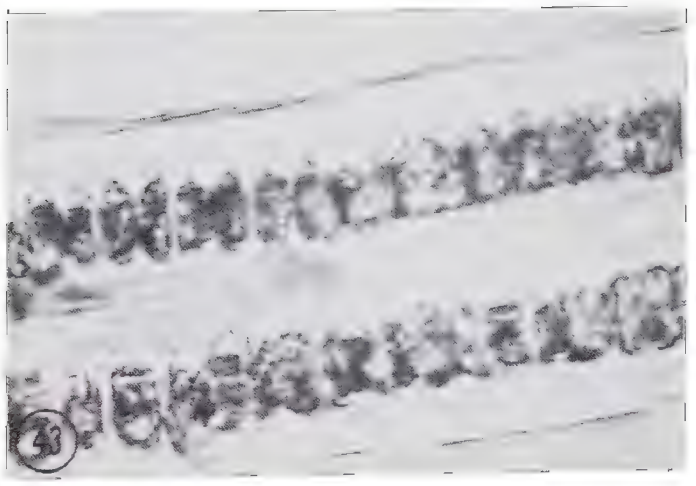
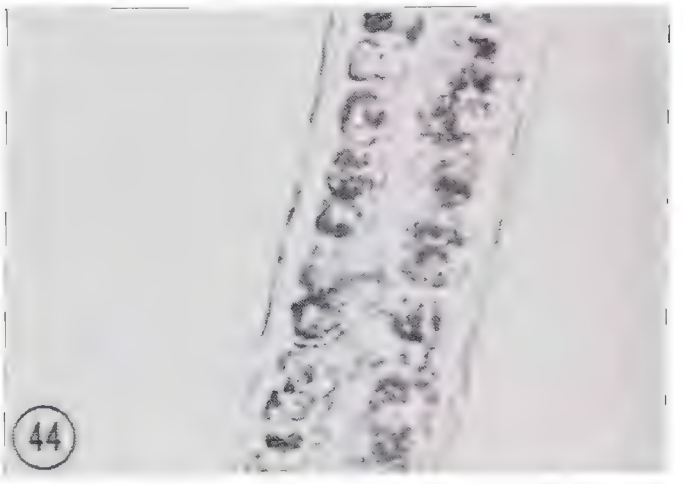

43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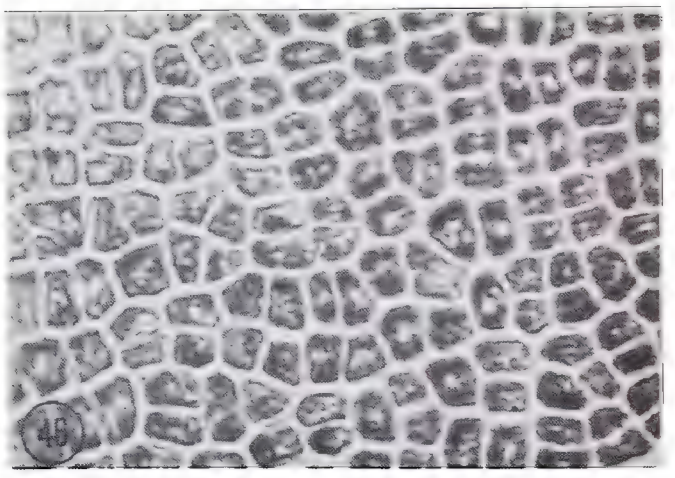
45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47

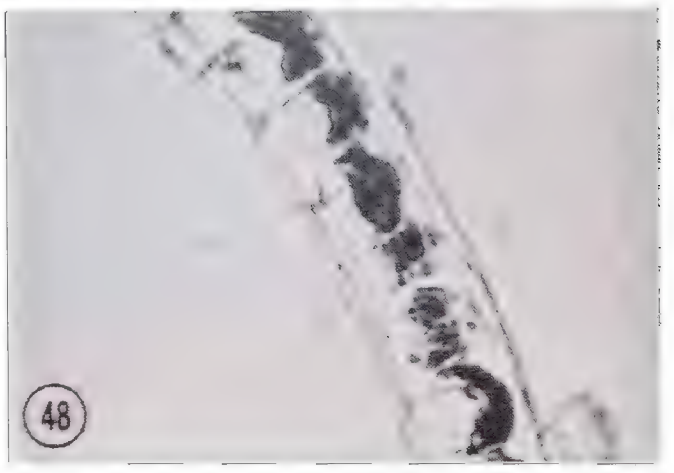
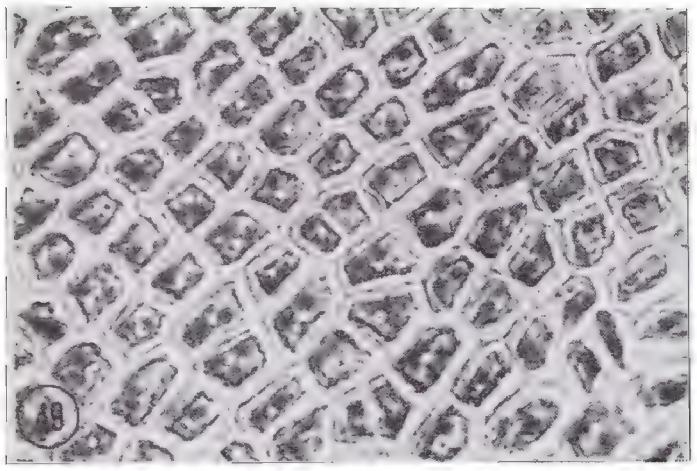

48

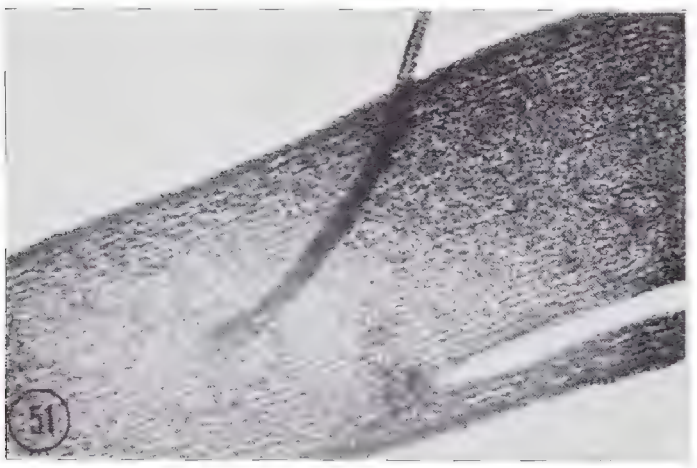
FIG. 41–48

Plants collected in nature.

FIG. 41. *Ulva fasciata* in surface view, 660x.
FIG. 42. *Ulva fasciata* in surface view, 300x.
FIG. 43. Transverse section of *Ulva fasciata* frond, 660x.
FIG. 44. Transverse section of *Ulva lactuca* frond, 500x.
FIG. 45. *Ulva lactuca* in surface view, 500x.
FIG. 46. *Enteromorpha ramulosa* in surface view, 300x.
FIG. 47. *Enteromorpha ramulosa* showing pattern of branching, 60x.
FIG. 48. Transverse section of *Enteromorpha ramulosa* frond, 660x.


49

50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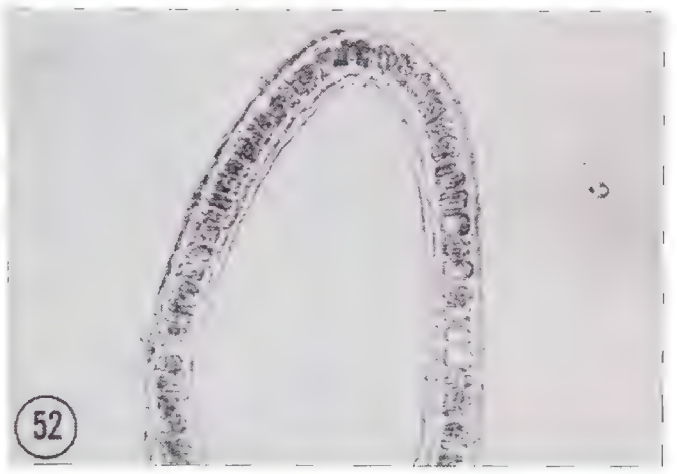
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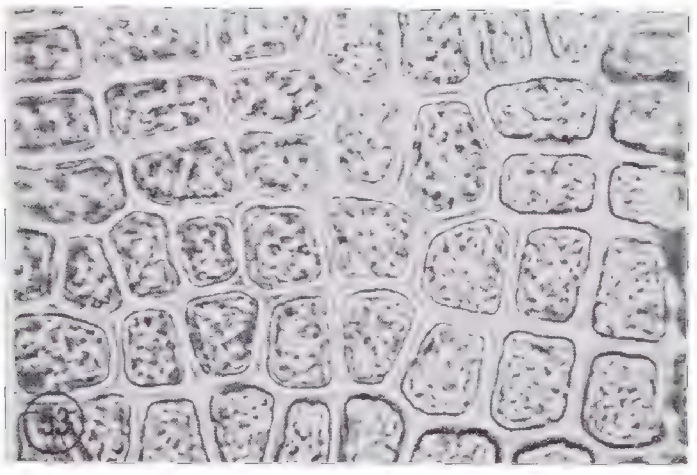
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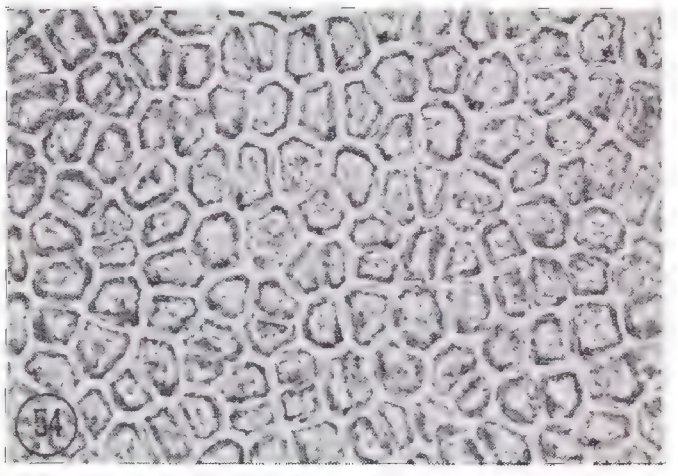
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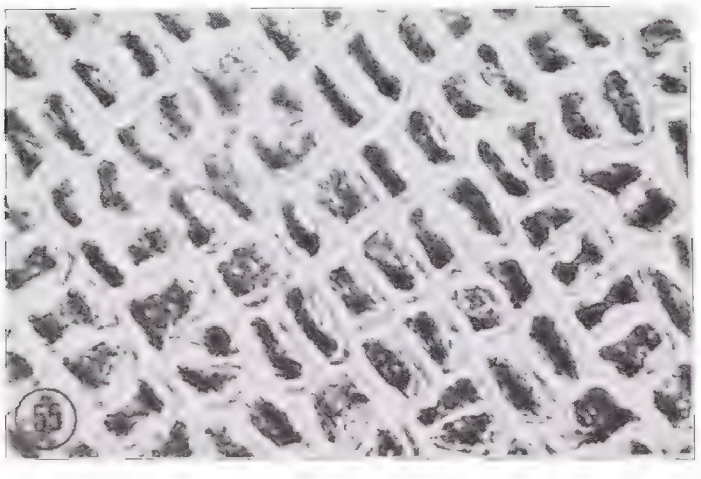
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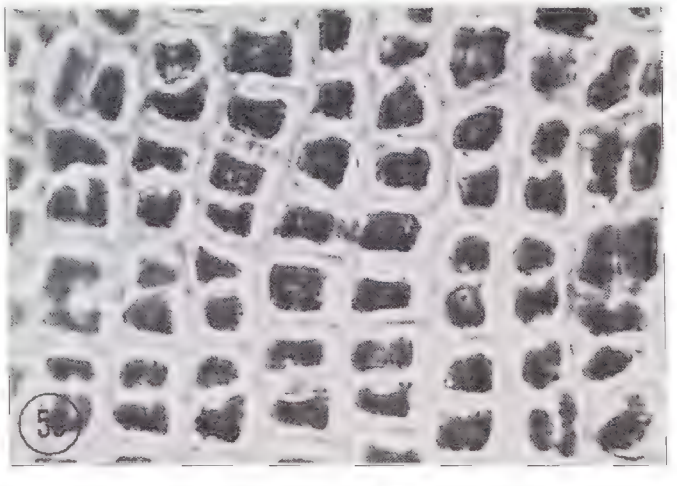

56

FIG. 49–56

Plants collected in nature.

FIG. 49. *Enteromorpha salina* in surface view, 300x.

FIG. 50. *Enteromorpha salina* in surface view, 300x.

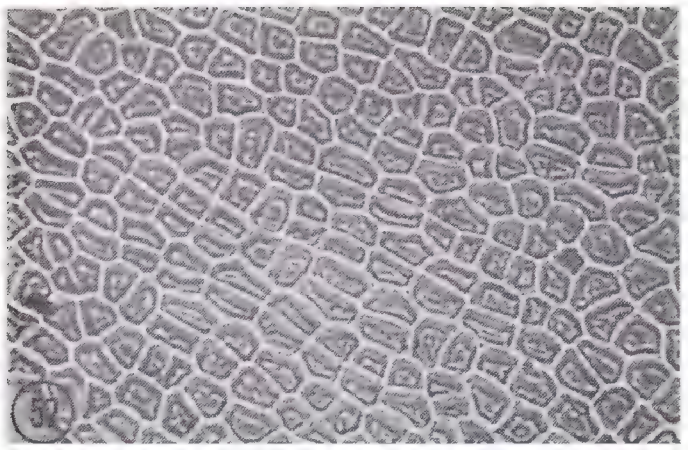
FIG. 51. *Enteromorpha salina* showing pattern of branching, 60x.

FIG. 52. Transverse section of *Enteromorpha flexuosa*, 200x.

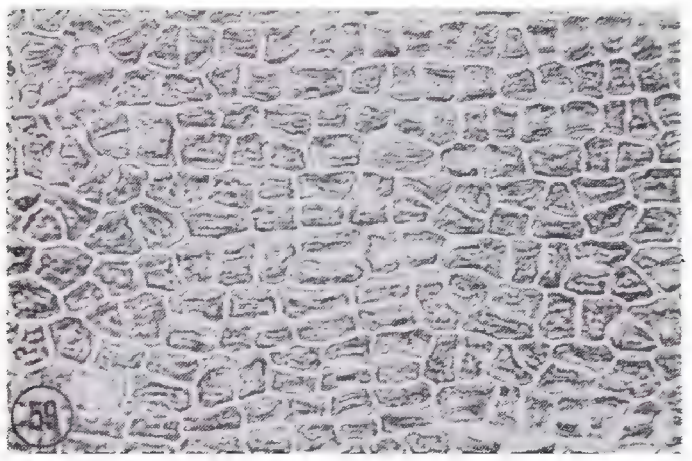
FIG. 53. *Enteromorpha flexuosa* in surface view, 500x.

FIG. 54. *Enteromorpha flexuosa* in surface view, 300x.

FIG. 55,56. *Enteromorpha lingulata* in surface view, 360x.


57

58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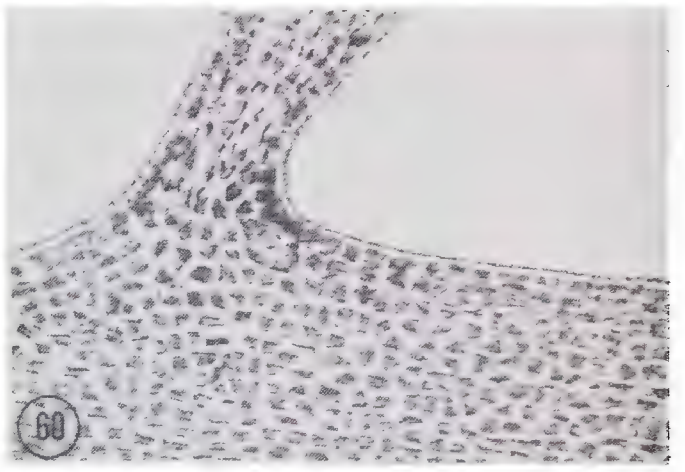
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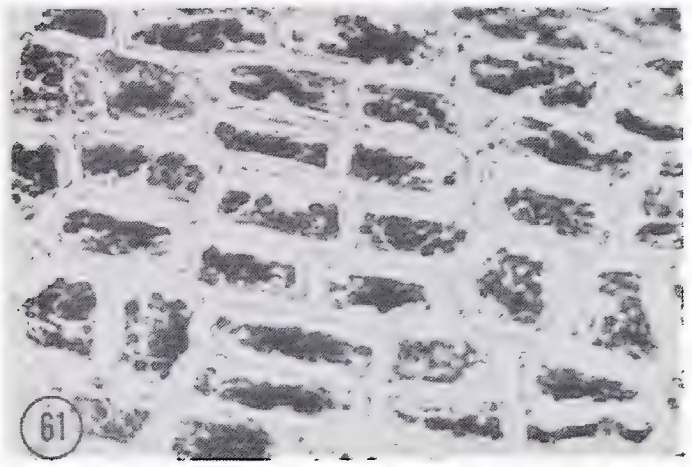

61

62

FIG. 57–62

Plants collected in nature.

FIG. 57. *Enteromorpha prolifera* in surface view, 360x.

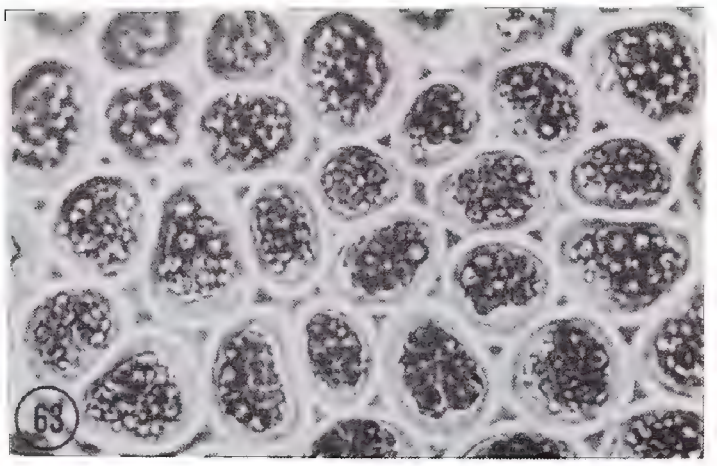
FIG. 58. *Enteromorpha prolifera* showing pattern of branching, 60x.

FIG. 59. *Enteromorpha prolifera* in surface view, 360x.

FIG. 60. *Enteromorpha clathrata* showing pattern of branching, 180x.

FIG. 61. *Enteromorpha clathrata* in surface view, 660x.

FIG. 62. *Enteromorpha clathrata* showing pattern of branching, 60x.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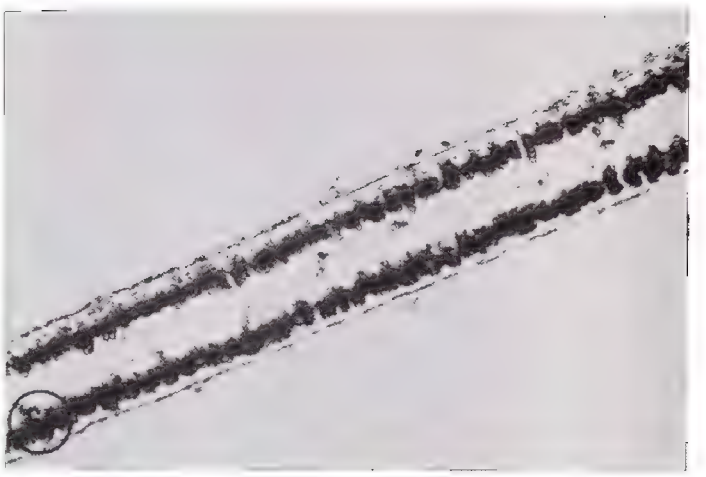
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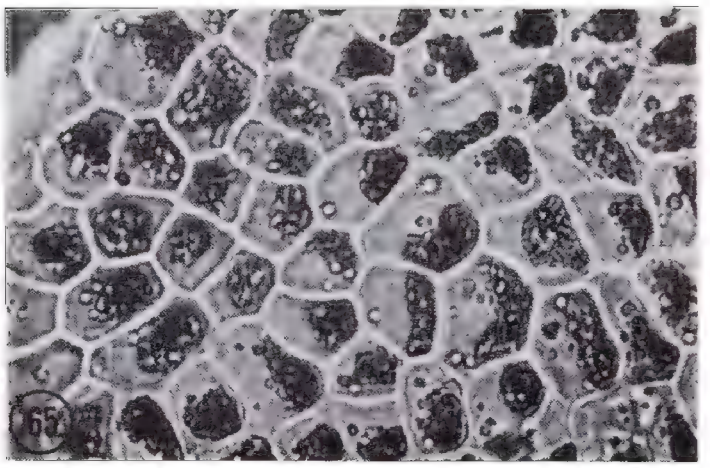
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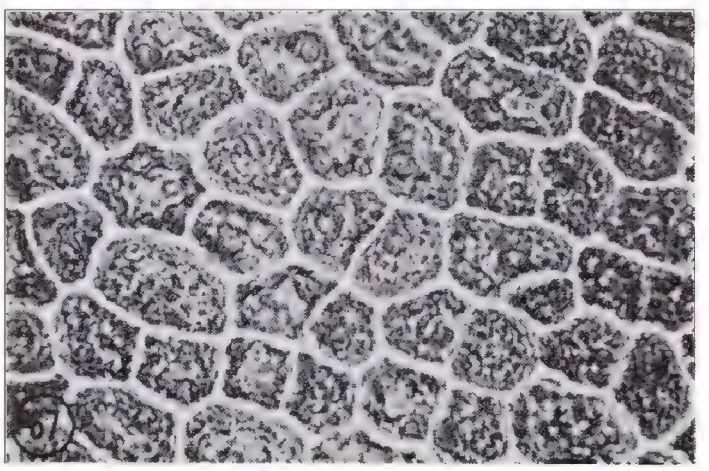
66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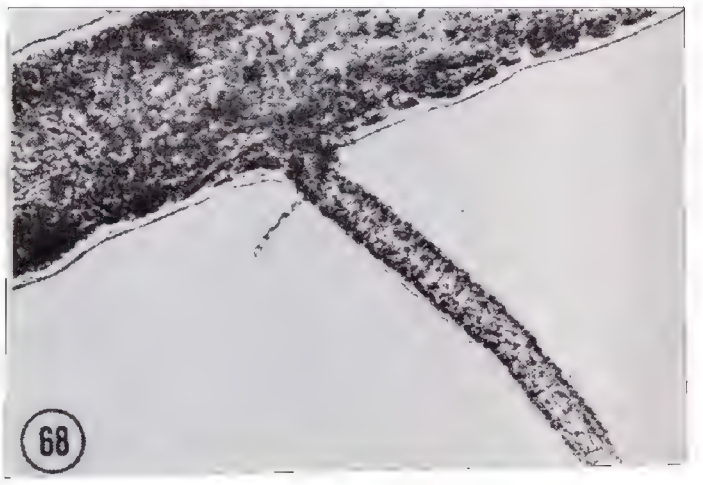
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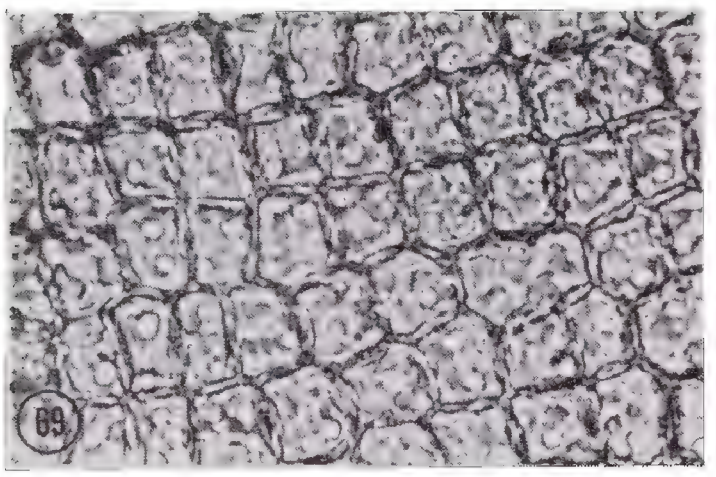
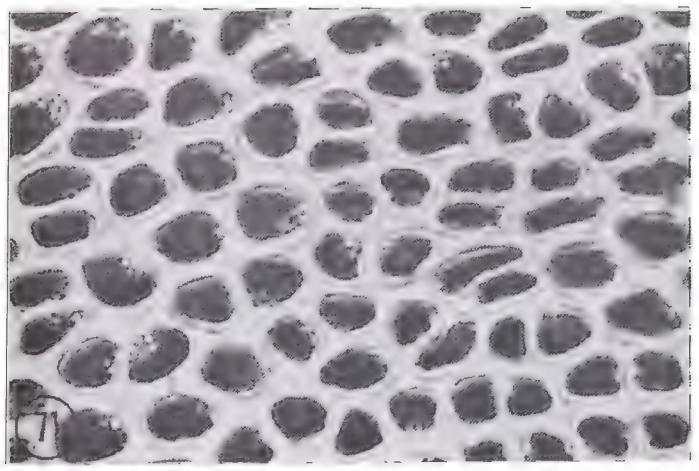

69

70

FIG. 63–70

Plants maintained in culture.

FIG. 63. *Ulva fasciata* in surface view, 660x.
FIG. 64. Transverse section of *Ulva fasciata* frond, 500x.
FIG. 65. *Ulva lactuca* in surface view, 660x.
FIG. 66. Transverse section of *Enteromorpha salina*, frond, 200x.
FIG. 67. *Enteromorpha salina* in surface view, 660x.
FIG. 68. *Enteromorpha salina* showing pattern of branching, 60x.
FIG. 69. *Enteromorpha ramulosa* in surface view, 660x.
FIG. 70. *Enteromorpha ramulosa* showing pattern of branching, 60x.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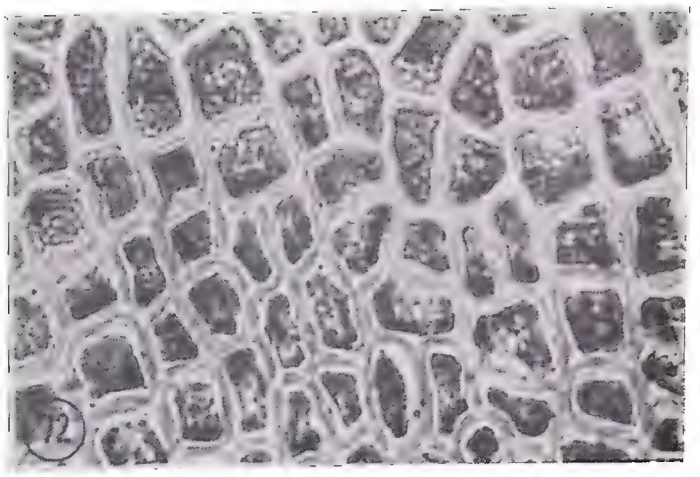
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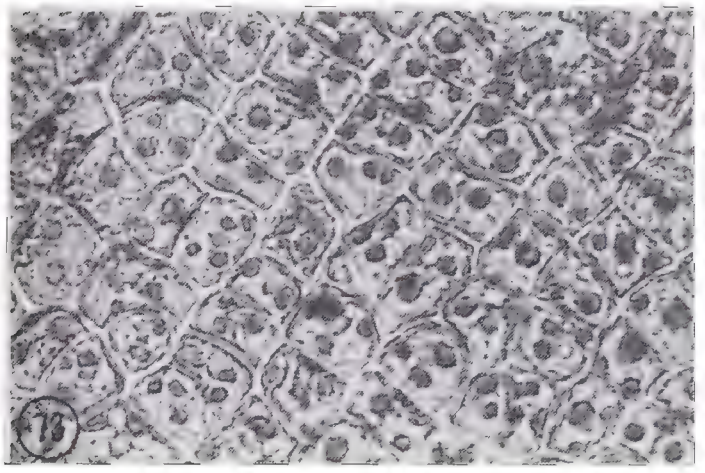
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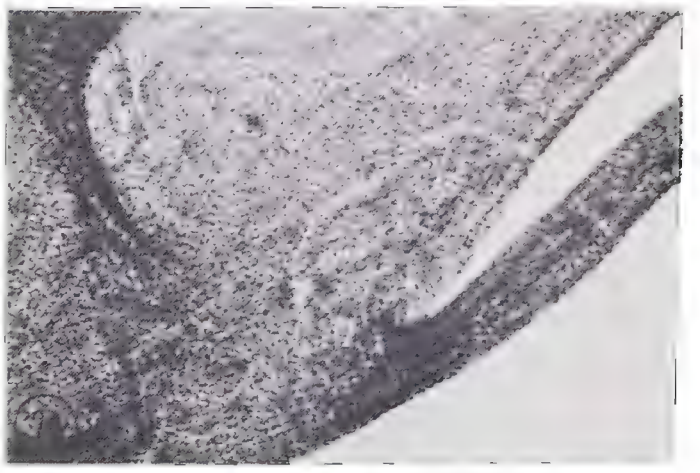
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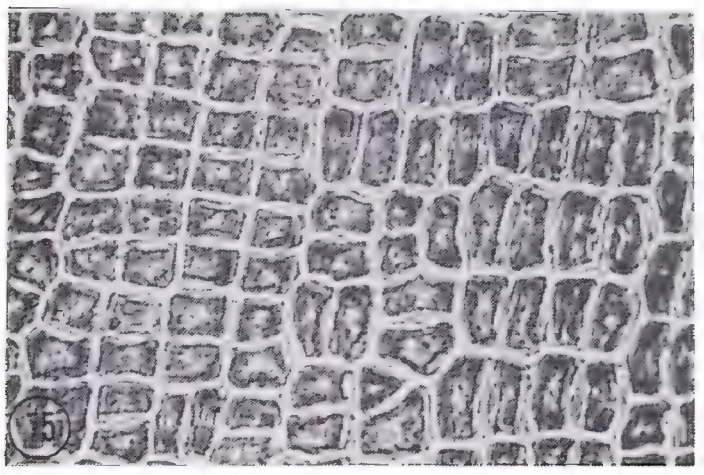
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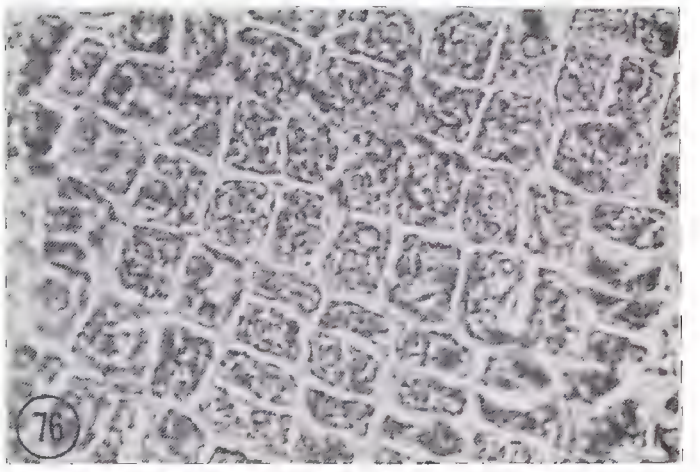
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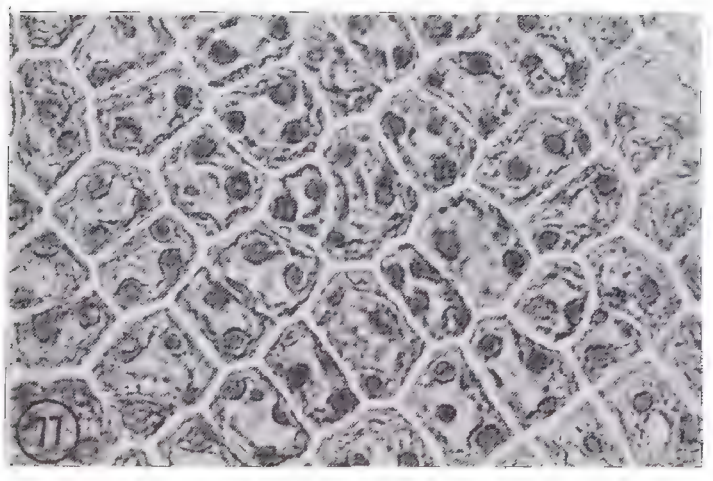
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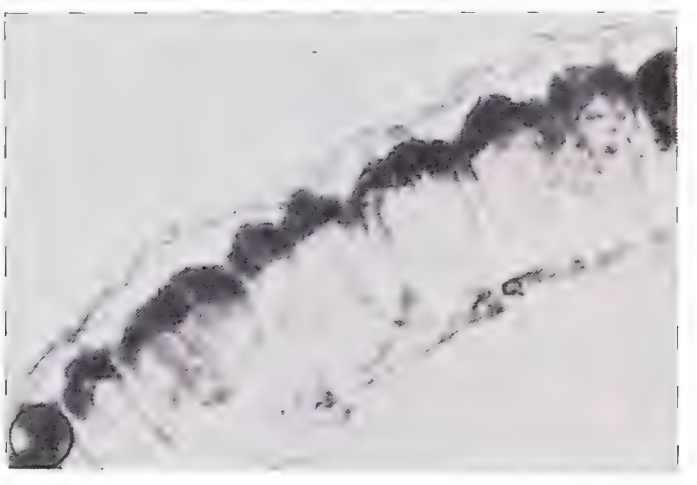
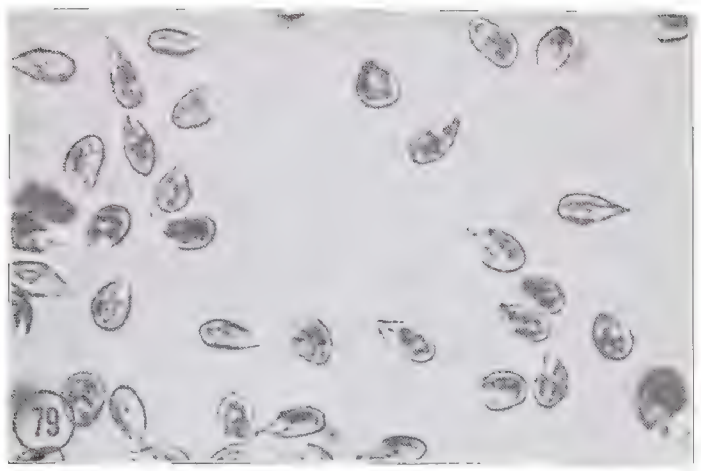


FIG. 71–78

Plants maintained in culture.

FIG. 71–73. *Enteromorpha prolifera* in surface view, 360x.
FIG. 74. *Enteromorpha prolifera* showing pattern of branching, 60x.
FIG. 75, 76. *Enteromorpha lingulata* in surface view, 360x.
FIG. 77. *Enteromorpha flexuosa* in surface view, 360x.
FIG. 78. Transverse section of *Enteromorpha flexuosa* frond, 660x.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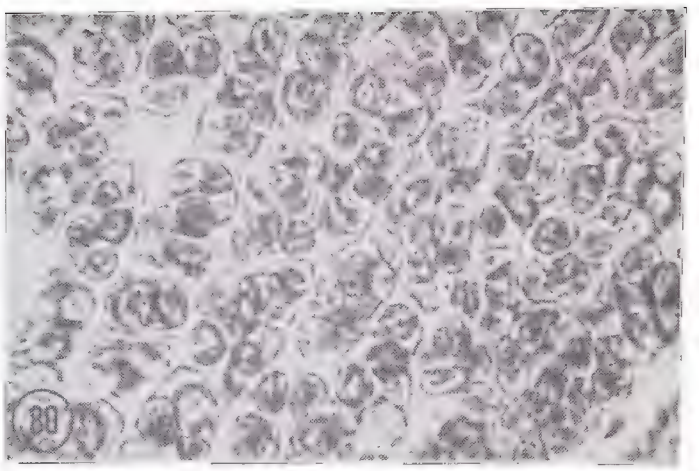
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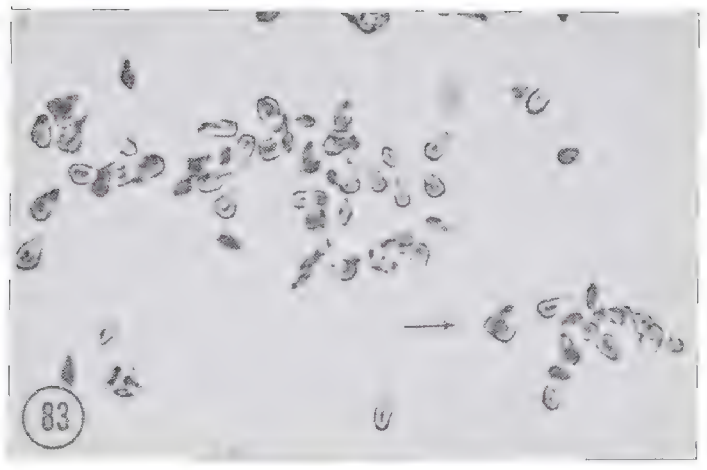
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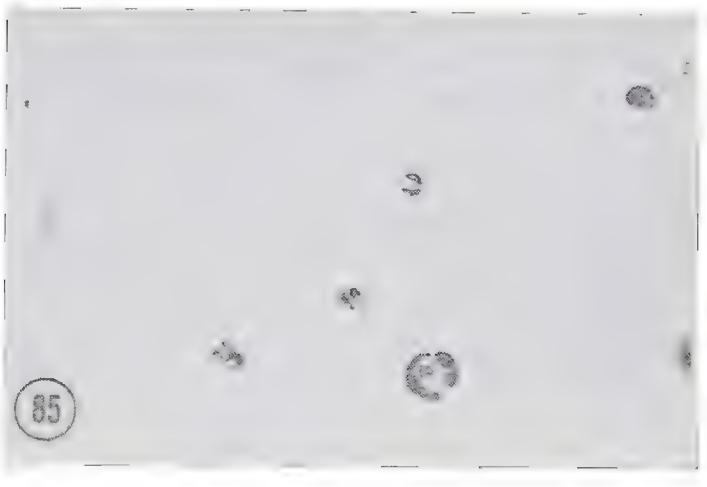

85

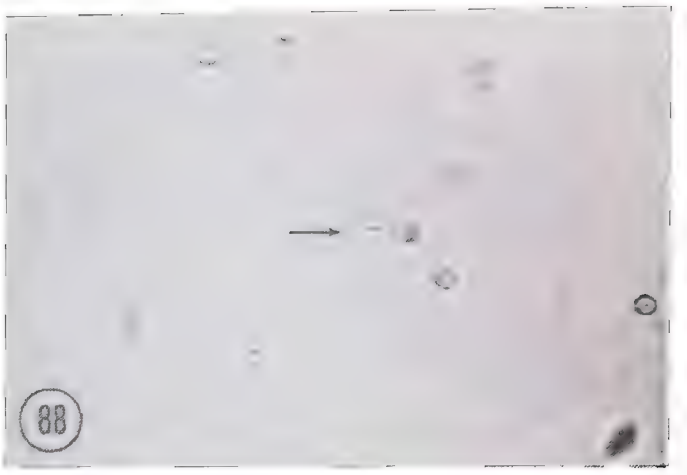
86

FIG. 79–86

Reproductive stages in *Enteromorpha.*

FIG. 79. Quadriflagellate zoospores of *Enteromorpha flexuosa*, 660x.
FIG. 80. Sporogenesis in *Enteromorpha prolifera*, 360x.
FIG. 81. Gamete release through pores in *Enteromorpha prolifera*, 360x.
FIG. 82. Quadriflagellate zoospores of *Enteromorpha prolifera*, 500x.
FIG. 83,84. Gametes of *Enteromorpha prolifera*, 500x.
FIG. 85. Zygotes of *Enteromorpha prolifera*, 660x.
FIG. 86. Germinating zygote of *Enteromorpha prolifera*, 660x.

87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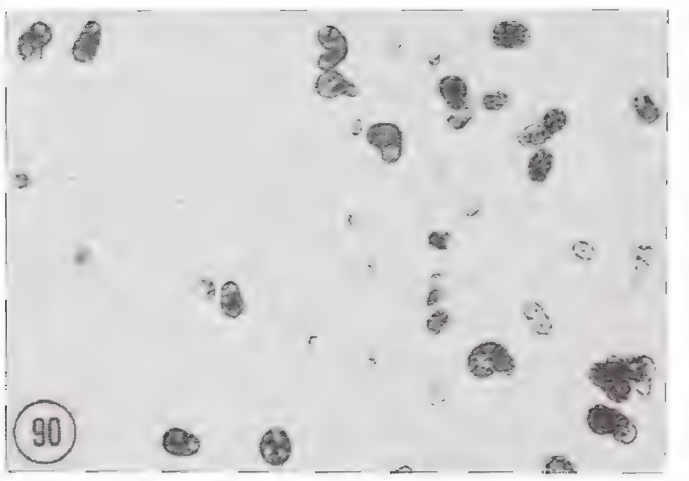
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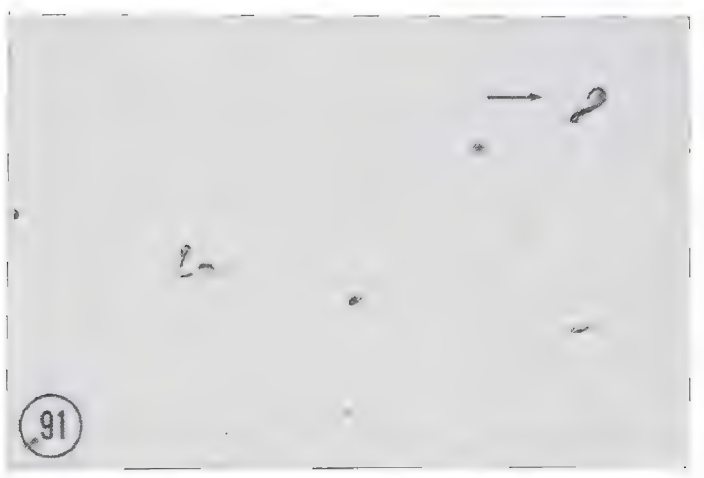
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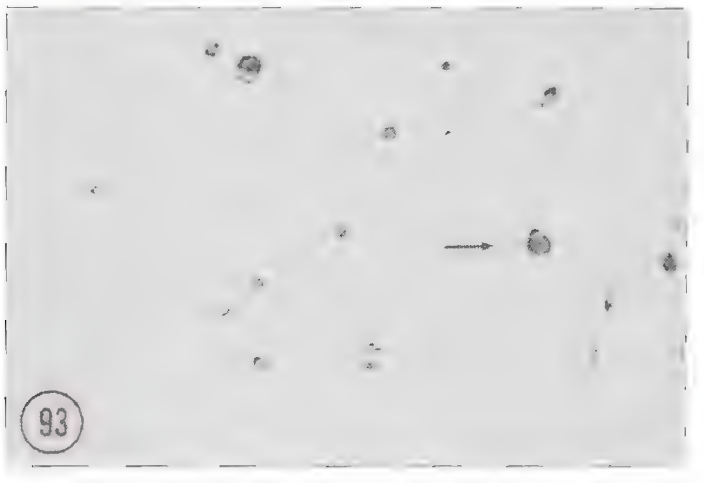
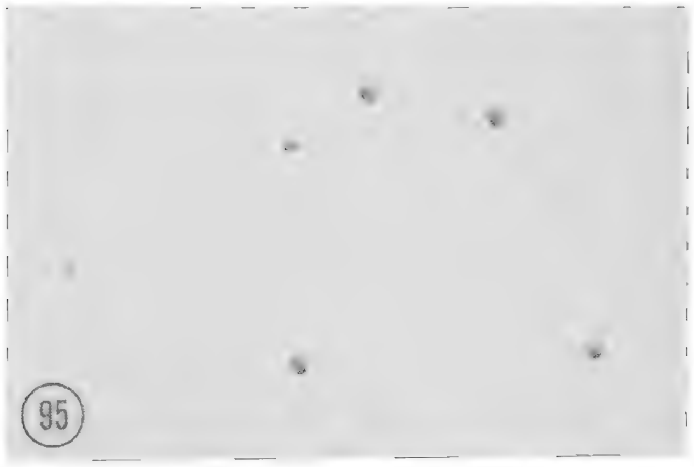

93

94

FIG. 87–94

Reproductive stages in *Enteromorpha* and *Ulva*.

FIG. 87–89. Gametes of *Enteromorpha clathrata*. Note pairing and fusing, 500x.
FIG. 90. Germinating zygotes of *Enteromorpha clathrata*, 500x.
FIG. 91. Gametes of *Ulva fasciata*. Note pairing and fusing, 360x.
FIG. 92. Zoospores of *Ulva fasciata*, 360x.
FIG. 93. Zygotes of *Ulva fasciata*, 360x.
FIG. 94. 10-day old germling of *Ulva fasciata*, 10x.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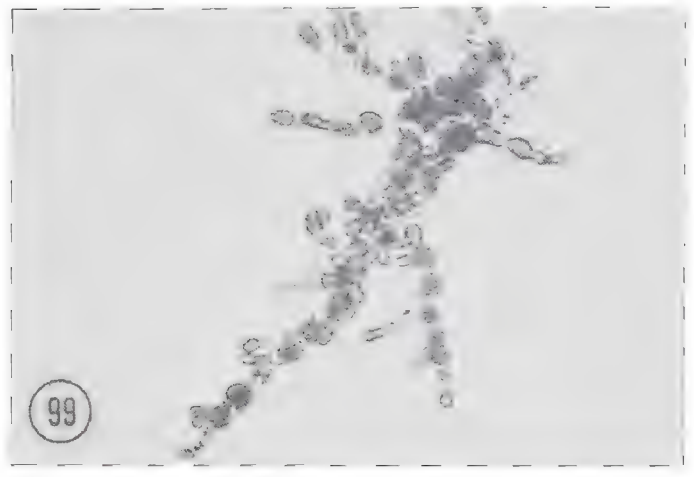
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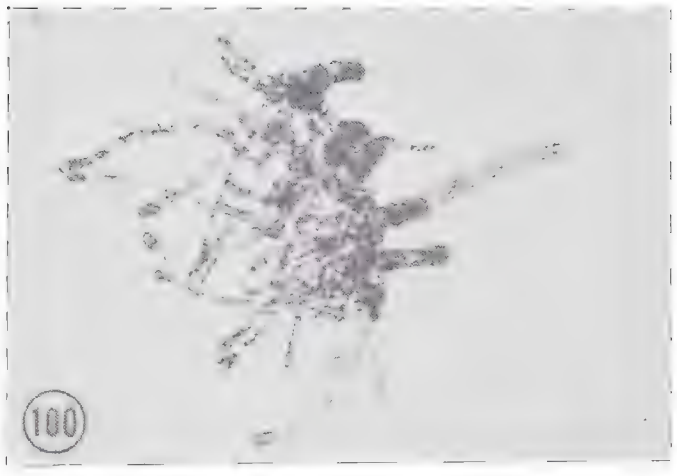

100

FIG. 95–100

Reproductive stages and germling development in *Enteromorpha* and *Ulva*.

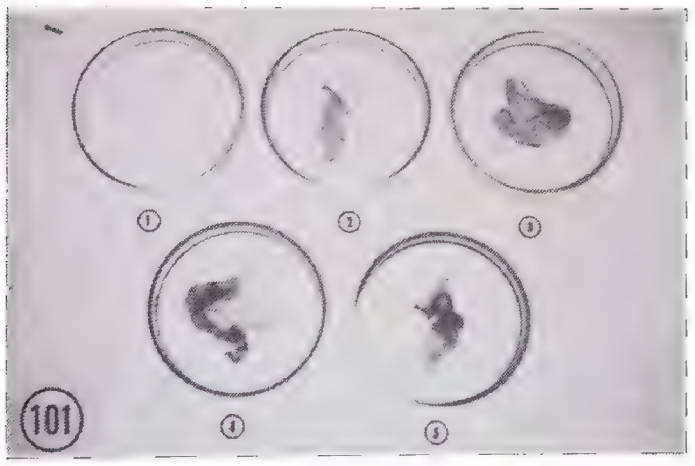
FIG. 95. Zoospores of *Enteromorpha ramulosa*, 360x.

FIG. 96. Zoospores of *Enteromorpha ramulosa* after settling, 660x.

FIG. 97. Germlings of *Ulva fasciata*, 360x.

FIG. 98. Germlings of *Enteromorpha lingulata*, 660x.

FIG. 99–100. Germlings of *Enteromorpha prolifera*, 360x.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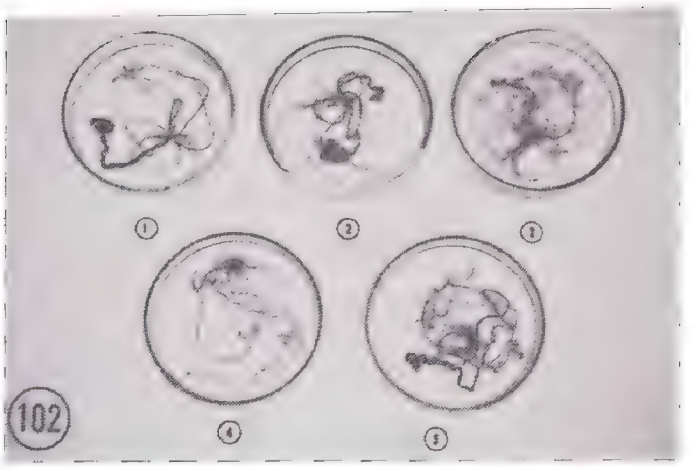
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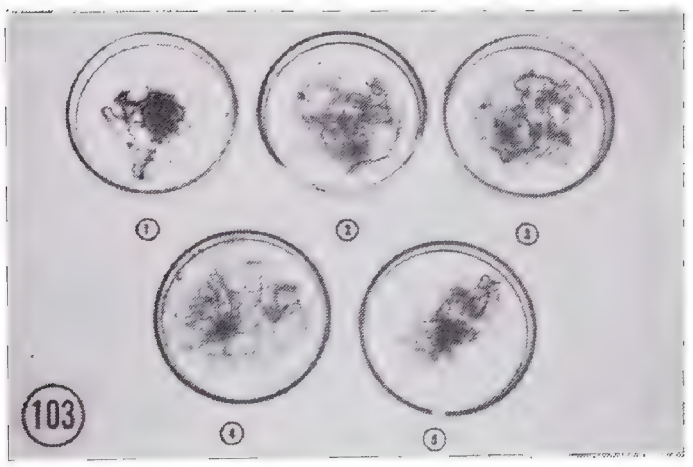
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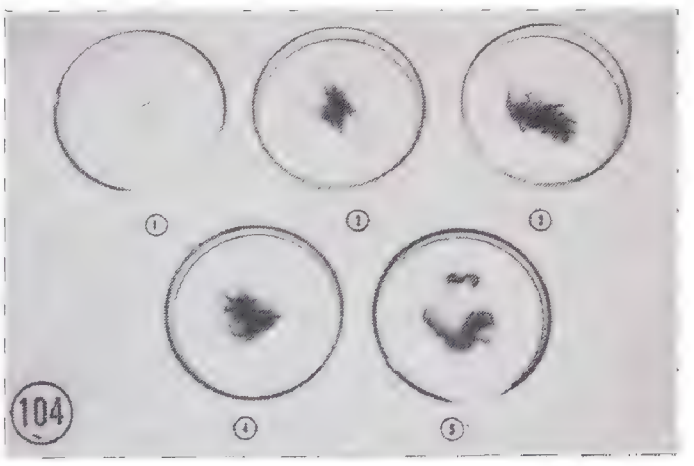
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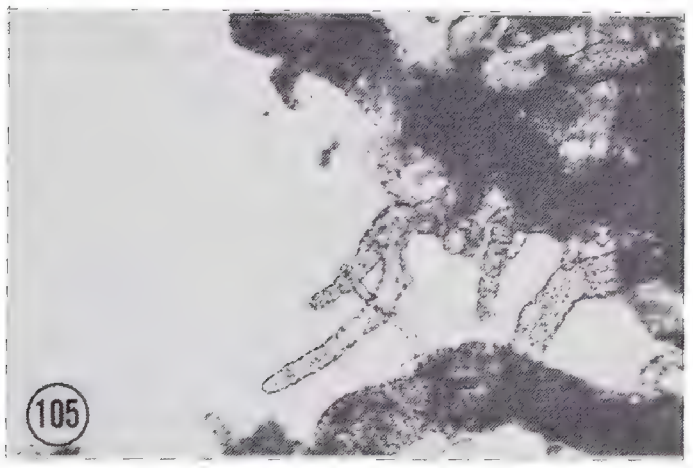
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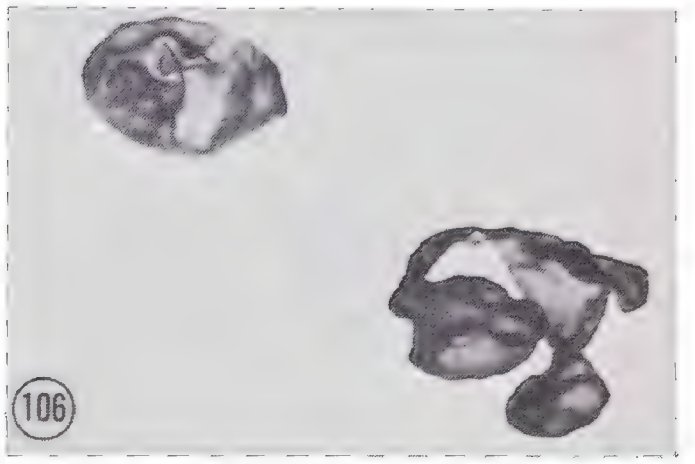
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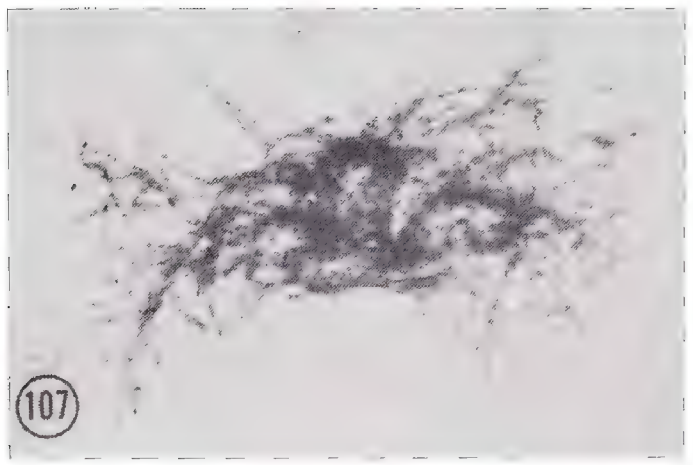
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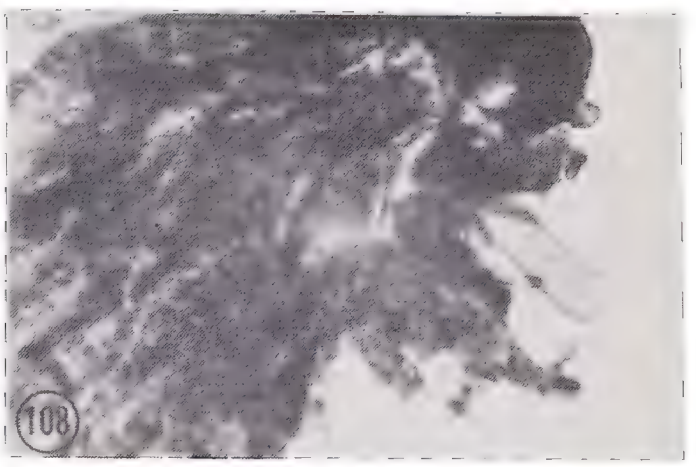
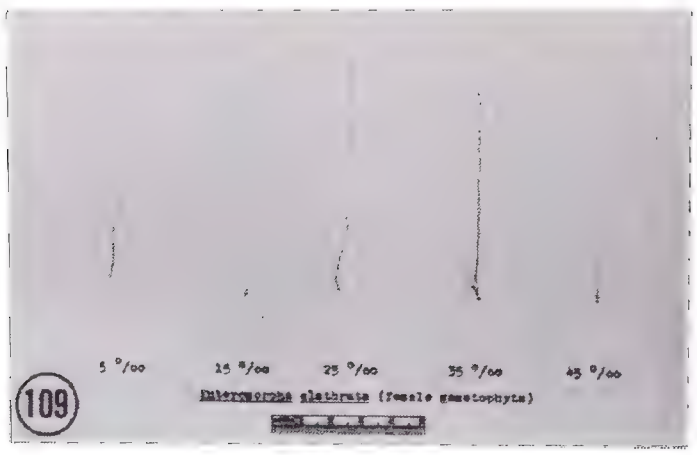

108

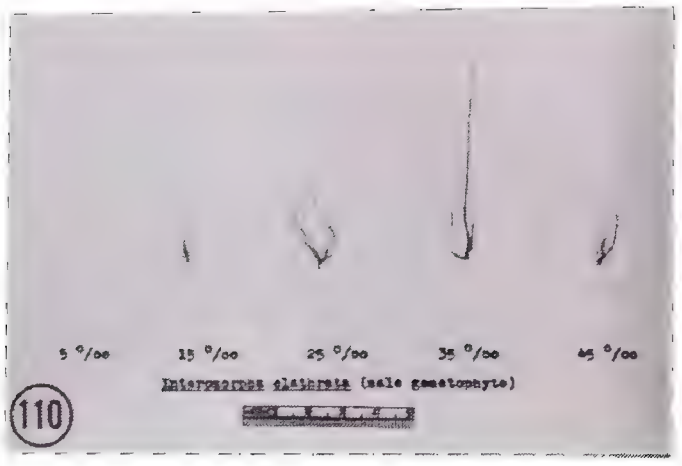
FIG. 101–104
Plants after 4 weeks in different temperature regimes: 1) 9 ± 1 2) 13 ± 2 3) 18 ± 2 4) 22 ± 2 5) 28 ± 2 C.

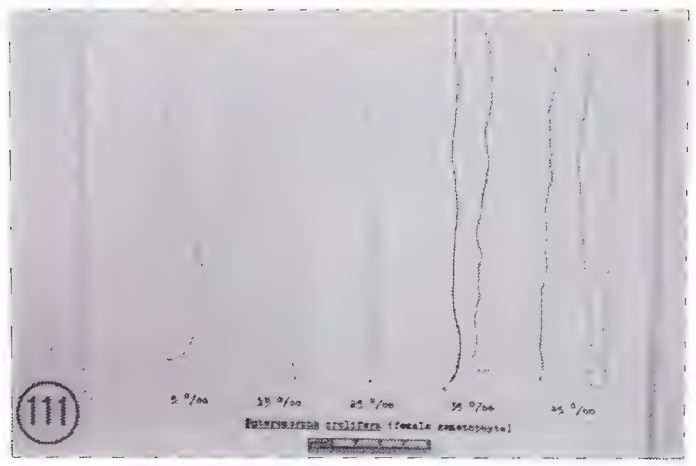
FIG. 101. *Ulva fasciata.*
FIG. 102. *Enteromorpha lingulata.*
FIG. 103. *Enteromorpha clathrata.*
FIG. 104. *Enteromorpha salina.*

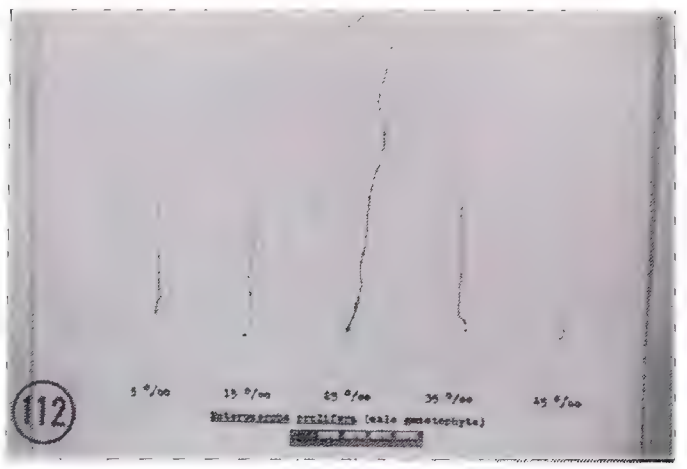
FIG. 105–108

FIG. 105. Frond of *Enteromorpha clathrata* after 4 weeks in Ott's artificial seawater, 120x.
FIG. 106. Fronds of *Ulva lactuca* after 4 weeks in Von Stosch's enriched seawater medium fortified with 2 N urea, 10x.
FIG. 107. Axenic frond of *Enteromorpha clathrata*, 60x.
FIG. 108. Axenic frond of *Ulva fasciata*, 60x.









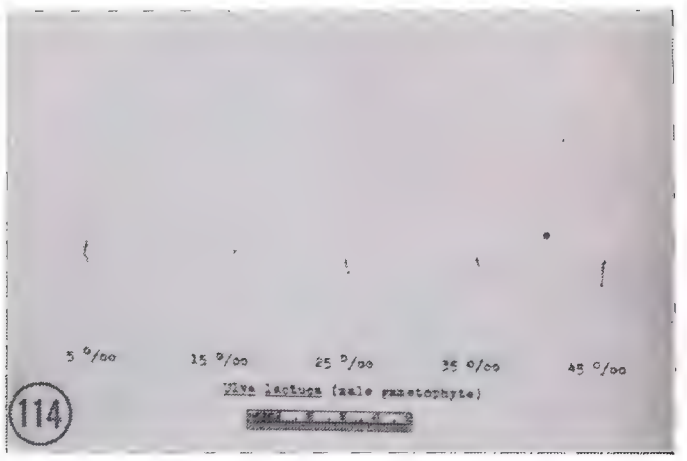
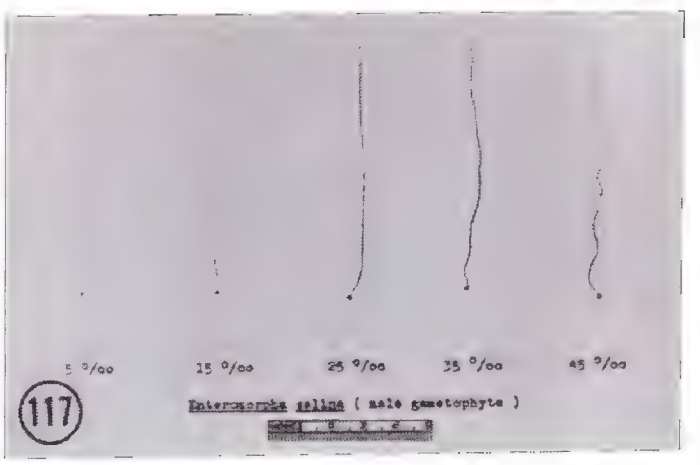
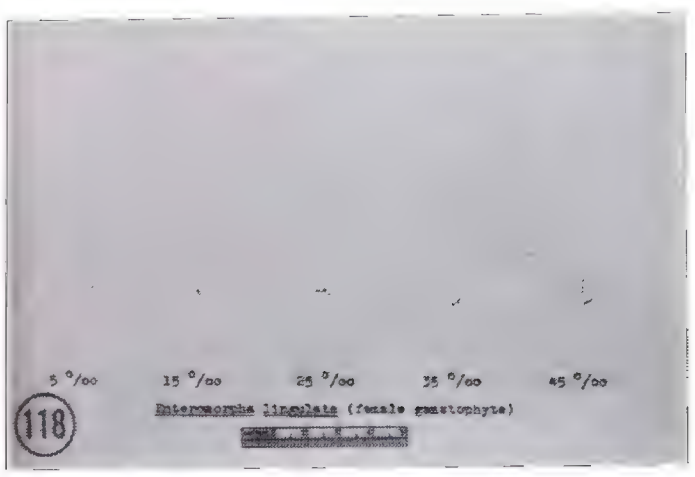
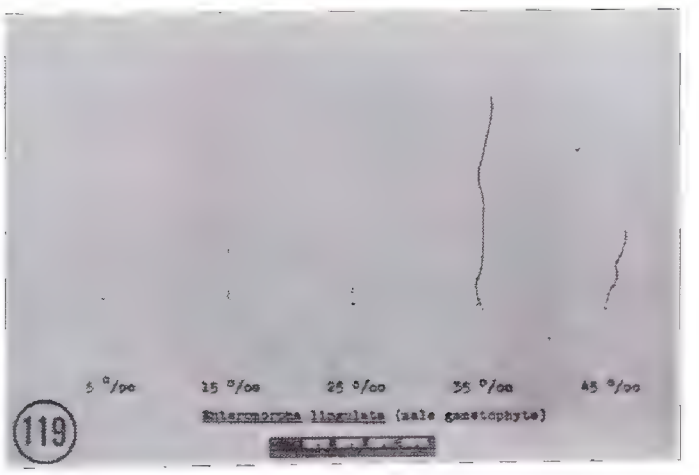
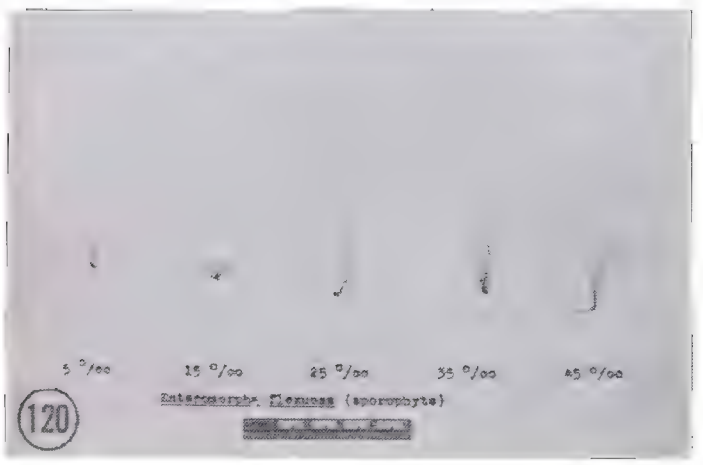


FIG. 109–115. Plants after 32 days in different salinity regimes.









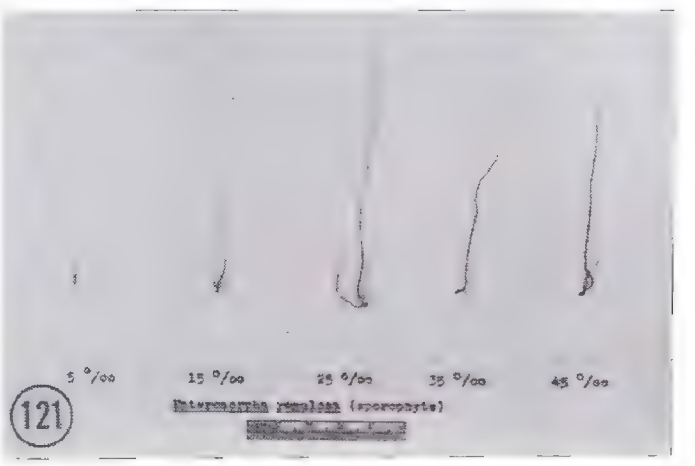
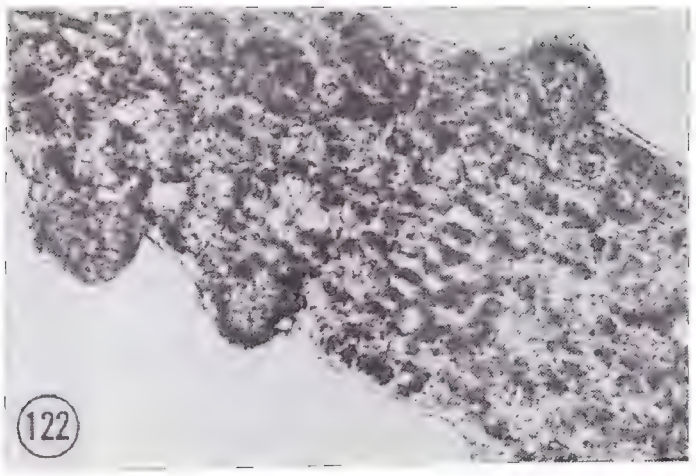
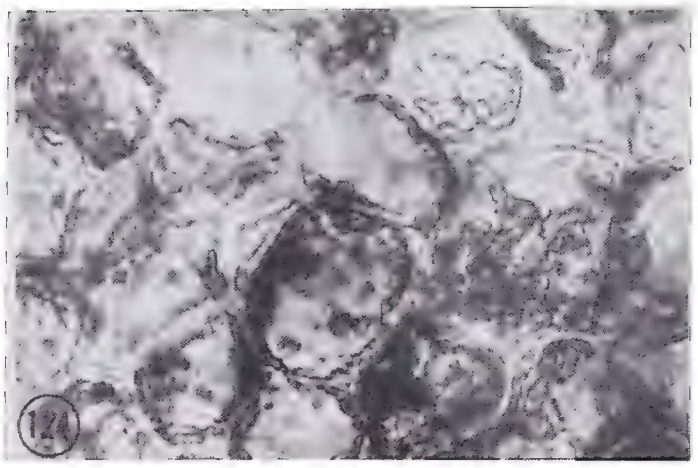


FIG. 116–121. Plants after 32 days in different salinity regimes.


122

123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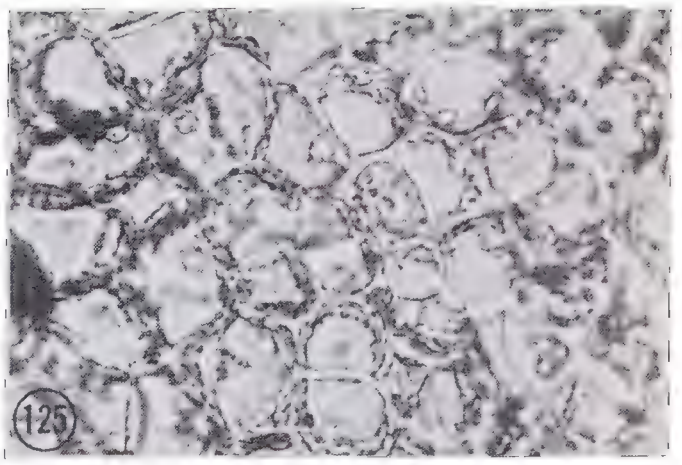
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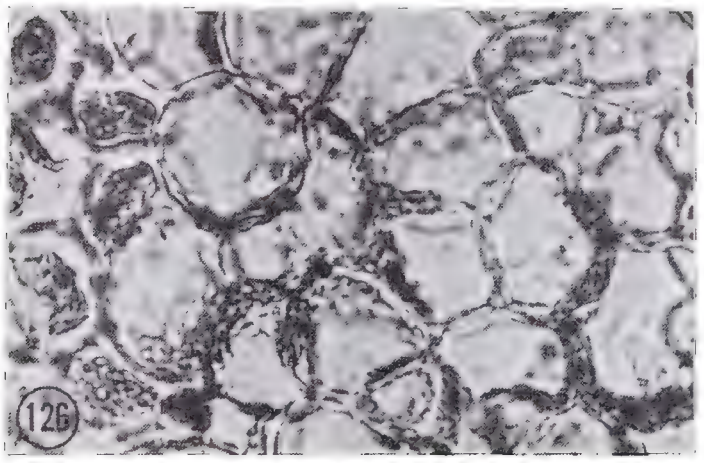
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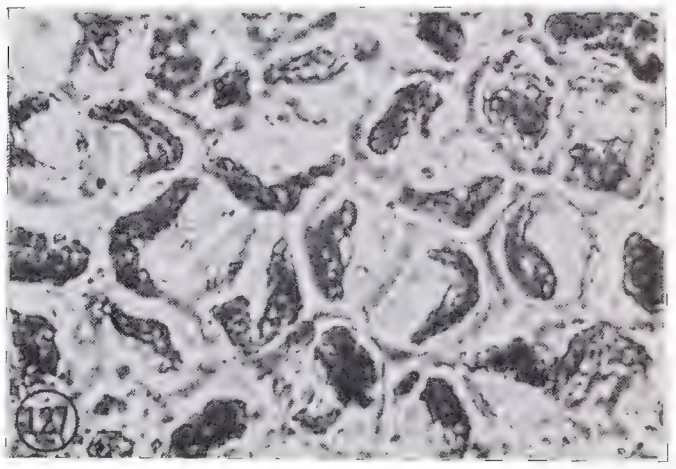
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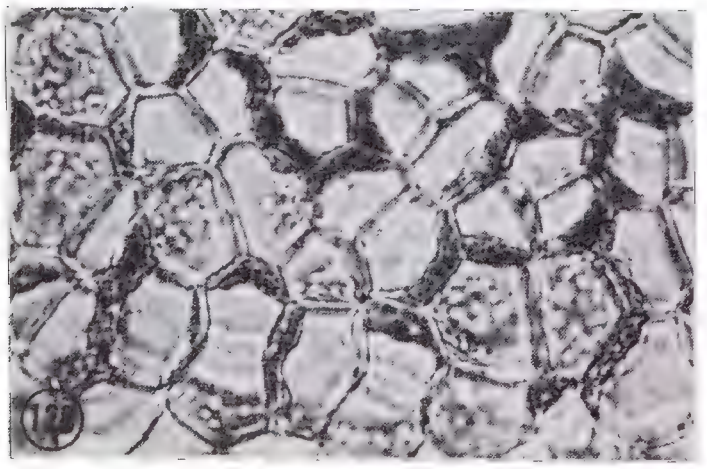
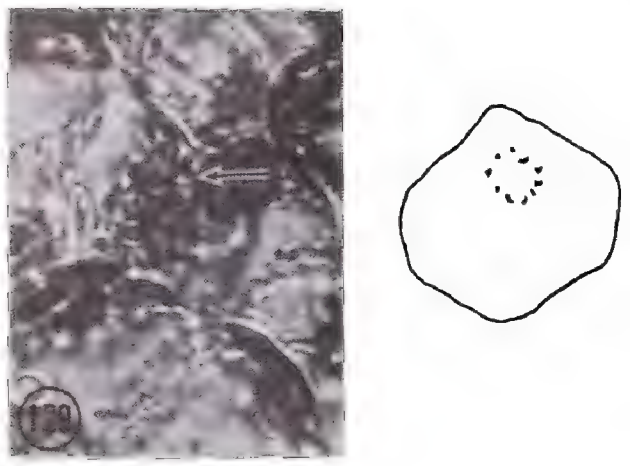
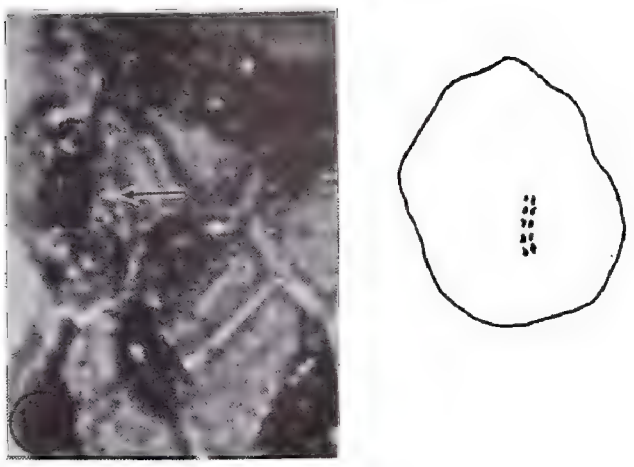
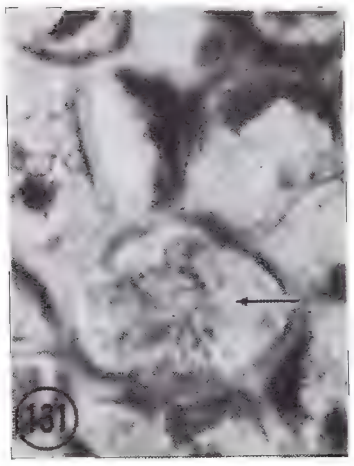
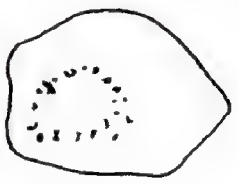
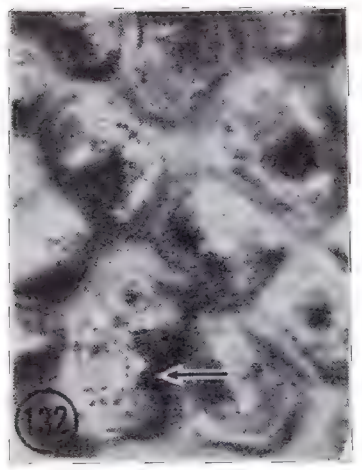
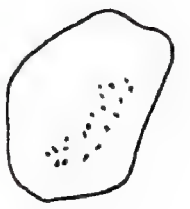
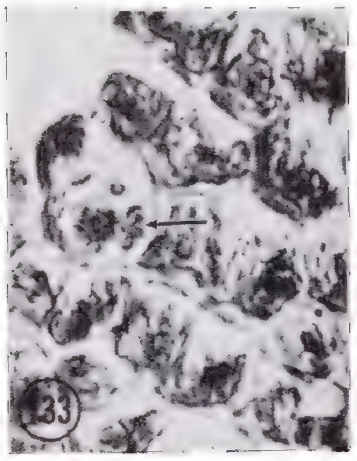
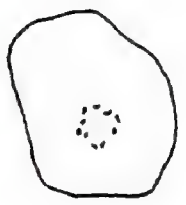
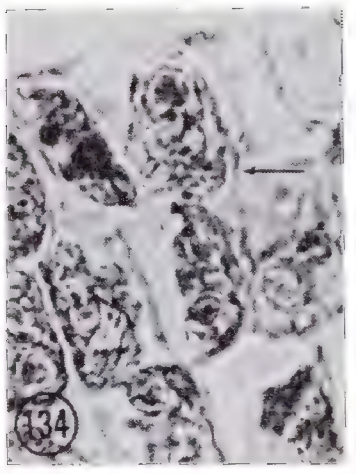

128

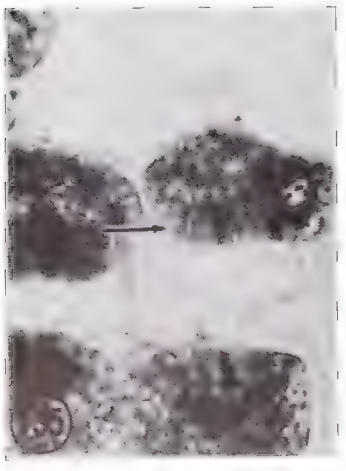
FIG. 122–128
Salinity studies.

FIG. 122. Frond of *Enteromorpha salina* after 4 weeks in a salinity of 7.5 ± 2.5 ‰, 60x.
FIG. 123. Frond of *Enteromorpha salina* after 4 weeks in a salinity of 50 ± 5 ‰, 120x.
FIG. 124–128. Surface views of *Ulva fasciata* fronds in salinities of 7.5 ± 2.5 ‰ (Fig. 124), 17.5 ± 2.5 ‰ (Fig. 125), 27.5 ± 2.5 ‰ (Fig. 126), 40 ± 5 ‰ (Fig. 127), 50 ± 5 ‰ (Fig. 128), 660x.







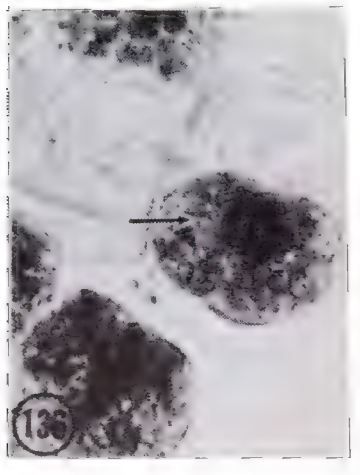


FIG. 129–136

Iron-alum aceto-carmine preparations of *Ulva* and *Enteromorpha* species.

FIG. 129. *Ulva fasciata.* Polar view of ring of 10 chromosomes in metaphase nucleus, 1000x.

FIG. 130. *Ulva fasciata.* Lateral view of 10 chromosomes in metaphase nucleus, 1000x.

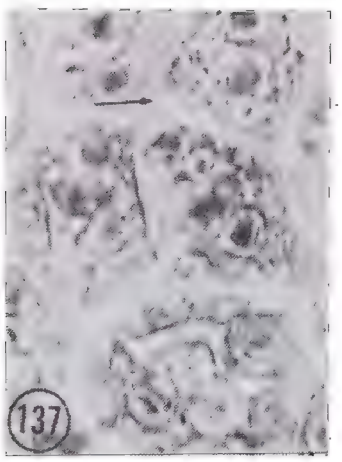
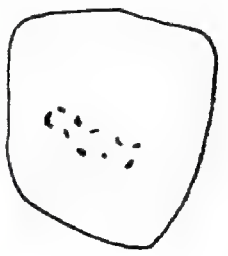
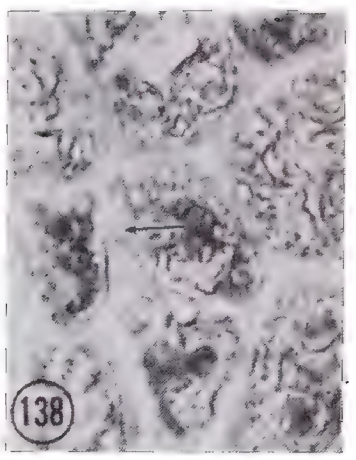
FIG. 131, 132. *Ulva fasciata.* Polar view of 20 chromosomes in diploid metaphase nucleus, 1000x.

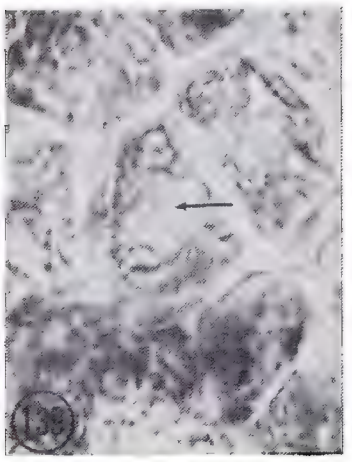
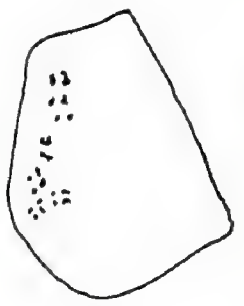
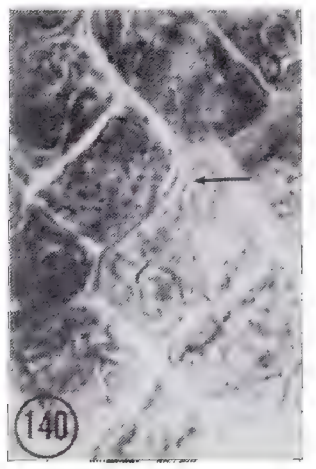
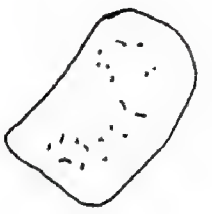
FIG. 133. *Ulva lactuca.* Polar view of ring of 10 chromosomes in metaphase nucleus, 660x.

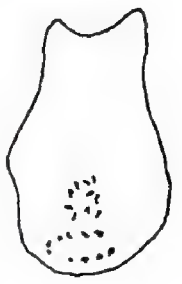
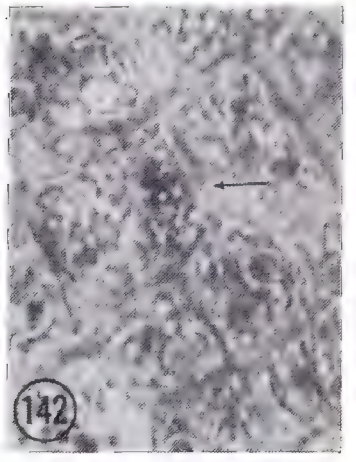
FIG. 134. *Enteromorpha lingulata.* Polar view of 10 chromosomes in metaphase nucleus, 1000x.

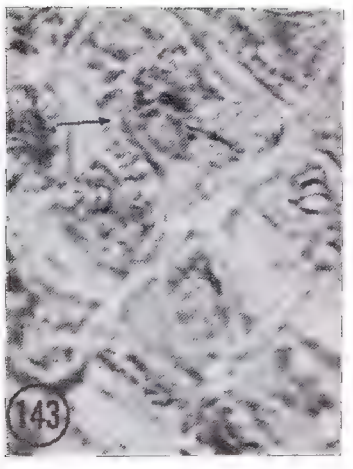
FIG. 135. *Enteromorpha clathrata.* Lateral view of two daughter nuclei in late anaphase showing two separate rings of 10 chromosomes, 1000x.

FIG. 136. *Enteromorpha clathrata.* Polar view of 10 chromosomes in metaphase nucleus, 1000x.



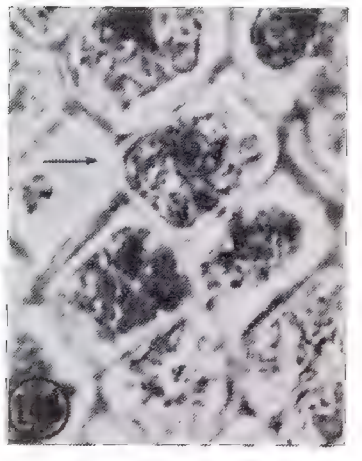
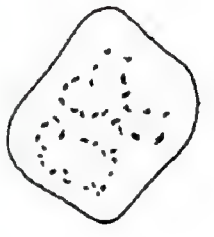



FIG. 137–144

Iron-alum aceto-carmine preparations of *Enteromorpha* species.

FIG. 137,138. *Enteromorpha flexuosa.* Polar view of 10 chromosomes in metaphase nucleus, 1000x.

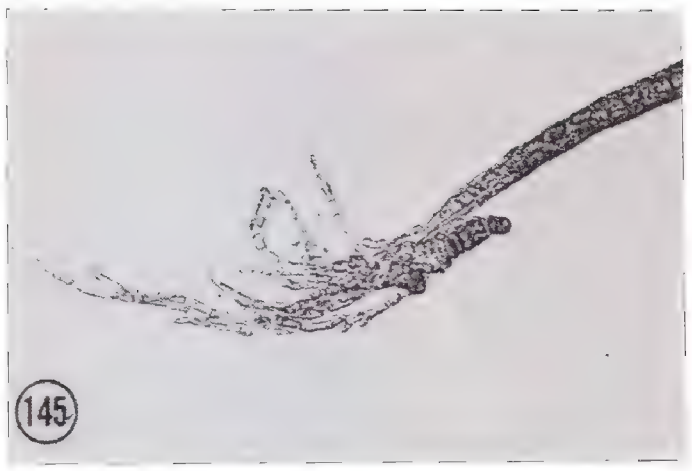
FIG. 139,140. *Enteromorpha ramulosa.* Polar view of 20 chromosomes in diploid metaphase nucleus, 1000x.

FIG. 141. *Enteromorpha prolifera.* Polar view of two daughter nuclei in early anaphase showing two separate rings of 10 chromosomes, 1000x.

FIG. 142. *Enteromorpha prolifera.* Polar view of 10 chromosomes in metaphase nucleus, 1000x.

FIG. 143. *Enteromorpha salina.* Polar view of 10 chromosomes in metaphase nucleus, 1000x.

FIG. 144. *Enteromorpha salina.* Polar view of tilted diploid nuclei in early anaphase, 1000x.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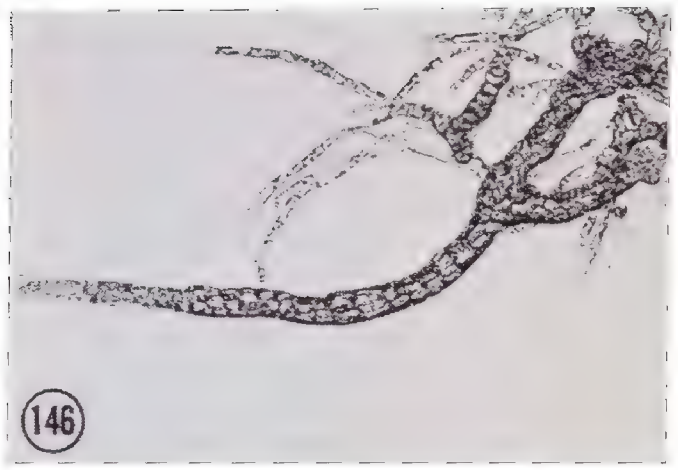
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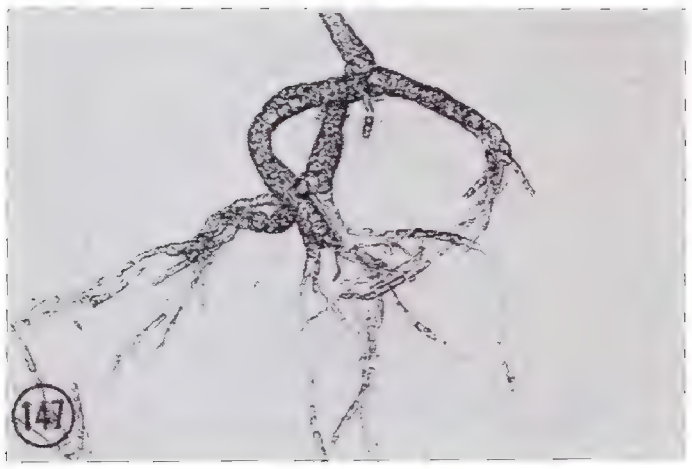
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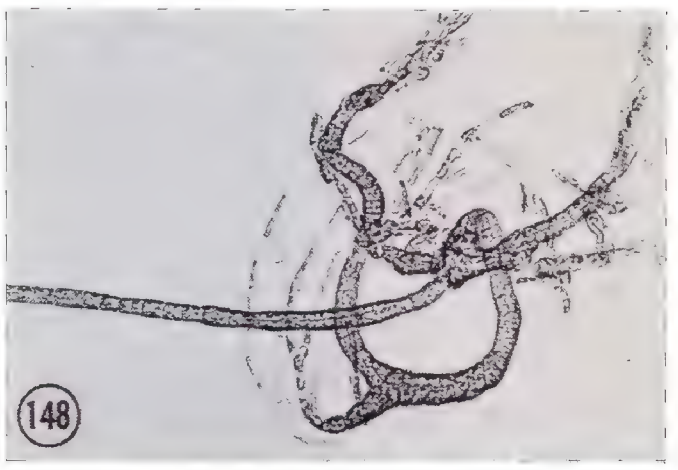
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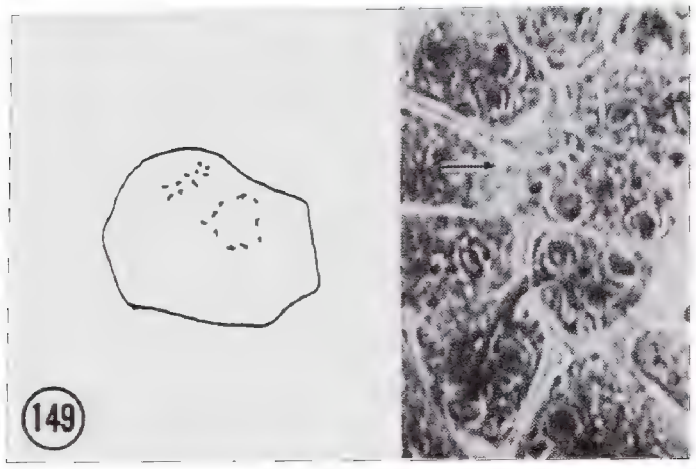
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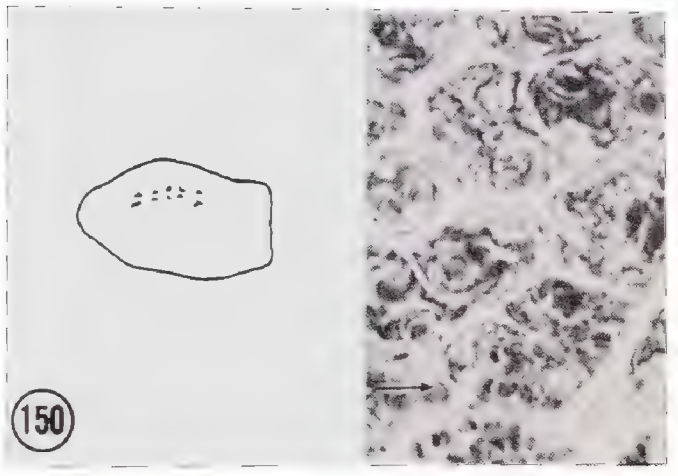
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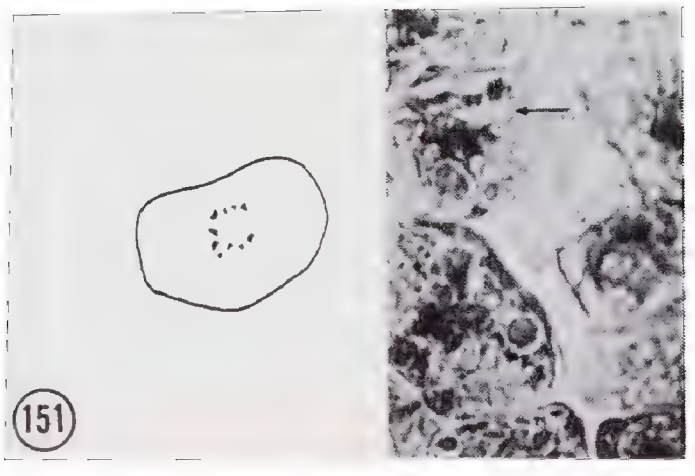
151

FIG. 145–148

Germling development.

FIG. 145. Normal germling arising from parthenogenetic female gamete of *Enteromorpha salina*, 120x.

FIG. 146–148. Y-shaped germlings arising from putative hybrids of *Enteromorpha salina* x *E. lingulata* (Fig. 146), *E. salina* x *E. prolifera* (Fig. 147), and *E. salina* x *E. clathrata* (Fig. 148), 120x.

FIG. 149–151

Iron-alum aceto-carmine preparations of putative hybrids.

FIG. 149. *Enteromorpha salina* x *E. lingulata*. Polar view of tilted nuclei in anaphase showing two separate rings of 10 chromosomes, 1000x.

FIG. 150. *Enteromorpha salina* x *E. prolifera*. Lateral view of 10 chromosomes in metaphase nucleus, 1000x.

FIG. 151. *Enteromorpha salina* x *E. clathrata*. Polar view of 10 chromosomes in metaphase nucleus, 1000x.

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